Departement für Kleintiere, Klinik für Zoo-, Heim- und Wildtiere
der Vetsuisse-Fakultät Universität Zürich

Direktor: Prof. Dr. med. vet. Jean-Michel Hatt

Arbeit unter wissenschaftlicher Betreuung von
Prof. Dr. med. vet. Marcus Clauss

Comparative omasum anatomy in ruminants: relationships with natural diet, digestive physiology, and general considerations on allometric investigations

Inaugural-Dissertation

zur Erlangung der Doktorwürde der
Vetsuisse-Fakultät Zürich

vorgelegt von

Christian-Frederic Ehrlich

Tierarzt
von Regensburg, Deutschland

genehmigt auf Antrag von

Prof. Dr. med. vet. Marcus Clauss, Referent
PD. Dr. med. vet. Karl Klisch, Korreferent

2018

Departement für Kleintiere, Klinik für Zoo-, Heim- und Wildtiere
der Vetsuisse-Fakultät Universität Zürich

Direktor: Prof. Dr. med. vet. Jean-Michel Hatt

Arbeit unter wissenschaftlicher Betreuung von
Prof. Dr. med. vet. Marcus Clauss

Comparative omasum anatomy in ruminants: relationships with natural diet, digestive physiology, and general considerations on allometric investigations

Inaugural-Dissertation

zur Erlangung der Doktorwürde der
Vetsuisse-Fakultät Zürich

vorgelegt von

Christian-Frederic Ehrlich

Tierarzt
von Regensburg, Deutschland

genehmigt auf Antrag von

Prof. Dr. med. vet. Marcus Clauss, Referent
PD. Dr. med. vet. Karl Klisch, Korreferent

2018

Inhaltsverzeichnis 3

1) Summary 4

2) Zusammenfassung 5

3) Abstract 7

4) Highlights (Graphical abstract) 8

5) Introduction
   - i) the omasum 9
   - ii) allometric investigation 11
   - iii) aims of the study 12

6) Methods
   - i) anatomical data sources 12
   - ii) measurments 13
   - iii) biological data 15
   - iv) allometric models and geometric effect 17
   - v) statistics and data presentation 17

7) Results
   - i) comparison between free-ranging and zoo specimens 19
   - ii) data visualisation 20
   - iii) allometric scaling and the natural diet 21
   - iv) allometric scaling, natural diet and intraruminal papillation 21
   - v) allometric scaling, natural diet and fluid throughput 22

8) Discussion
   - i) limitations 23
   - ii) effects of phylogeny 25
   - iii) mathematical approach to testing influence on allometries 25
   - iv) forestomach physiology and diet niche 27
   - v) omasum development 29
   - vi) conclusion and outlook 32

9) Additional material 33

10) References 33-39

11) Table (1-3) 40-44

12) Graphs with supplementary material 45-63

13) Curriculum Vitae

Vetsuisse-Fakultät Universität Zürich (2018)
Christian-Frederic Ehrlich
Klinik für Zoo-, Heim- und Wildtiere ehuber@vetclinics.uzh.ch

Comparative omasum anatomy in ruminants: relationships with natural diet, digestive physiology, and general considerations on allometric investigations

Abstract

The omasum is the third forestomach compartment of pecoran ruminants. It is assumed that its main function is the re-absorption of fluid, so that less diluted digesta is submitted to enzymatic digestion in the lower digestive tract. Here, we evaluate measures of omasum size (84 ruminant species in the largest dataset) against body mass and proxies of the natural diet (%grass) or forestomach physiology (fluid throughput), using phylogenetically controlled models. Models with the best support invariably either included %grass or a physiology proxy in addition to body mass. These effects were not necessarily additive, but often indicated a change in the allometric body mass-exponent with diet or physiology. Only models that allowed an influence on the allometric exponent yielded basic exponents compatible with predictions derived from geometry. Species with more grass in their natural diet, or that have a 'cattle-type' physiology marked by a high forestomach fluid throughput, generally have larger omasa. However, the existence of outliers, as well as the overall data pattern, suggest that this is not an obligatory morphophysiological condition. Circumstantial evidence is presented leading to the hypothesis that the comparatively small and less complex omasa of 'moose-type' species may be derived from more complex states by ontogenetic reduction and fusion of omasal laminae.

Key words: Rumination, Digesta washing, Feeding niche, 'Moose-type', 'Cattle-type'

Vetsuisse-Fakultät Universität Zürich (2018)
Christian-Frederic Ehrlich
Klinik für Zoo-, Heim- und Wildtiere ehuber@vetclinics.uzh.ch

Comparative omasum anatomy in ruminants: relationships with natural diet, digestive physiology, and general considerations on allometric investigations

Zusammenfassung

Der Blättermagen ist die dritte Kammer des Vormagensystems von Wiederkäuern. Seine Hauptfunktion besteht in der Resorption von Flüssigkeit, damit weniger verdünntes Futter zur enzymatischen Verdauung in den weiteren Verdauungstrakt gelangt. Wir vergleichen Grössenverhältnisse von Blättermägen (von bis zu 84 Arten) mit der Körpermasse, der natürlichen Nahrung (%Gras) und der Vormagenphysiologie (Flüssigkeitsdurchsatz) anhand phylogenetischer statistischer Modelle. Die besten Modelle beinhalten stets entweder %Gras oder einen physiologischen Parameter zusätzlich zur Körpermasse. Die Variablen beeinflussen seltener die Höhe des Faktors, mit dem die skalierte Körpermasse mit dem Blättermagen korreliert, sondern öfter die Veränderung des Exponenten, mit dem Körpermasse zum Blättermagen skaliert. Nur Modelle, die solch eine Beeinflussung des Exponenten erlauben, resultieren in Basis-Exponenten, die geometrischen Vorhersagen entsprechen. Arten, deren natürliche Nahrung mehr Gras beinhaltet, oder die eine ‚cattle-type'-Physiologie aufweisen (mit höherem Flüssigkeitsdurchsatz), haben generell grössere Blättermägen. Ausreisser sowie das Datenmuster deuten darauf hin, dass dies keine obligatorische morphophysiologische Anpassung ist. Makroanatomische Beobachtungen führen zu der Hypothese, dass der verhältnismässig kleinere und weniger komplexe Blättermagen von ‚moose-type'-Arten ein abgeleitetes und kein ursprüngliches Merkmal darstellt.

Stichwörter: Blättermagen, cattle-type, moose-type

Comparative omasum anatomy in ruminants: relationships with natural diet, digestive physiology, and general considerations on allometric investigations

Christian Ehrlich[1], Daryl Codron[2,3], Reinhold R. Hofmann[4], Jürgen Hummel[5], Marcus Clauss[1,*]

[1]Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland, mclauss@vetclinics.uzh.ch

[2]Florisbad Quaternary Research Department, National Museum, PO Box 266, Bloemfontein, 9300, South Africa, darylcodron@gmail.com

[3]Centre for Environmental Management, University of the Free State, PO Box 339, Bloemfontein, 9300, South Africa

[4]Trompeterhaus, 15837 Baruth/Mark, Germany, trompeterhaus@t-online.de

[5]Ruminant Nutrition, Department of Animal Sciences, University of Goettingen, Kellnerweg 6, 37077 Goettingen, Germany, jhummel@gwdg.de

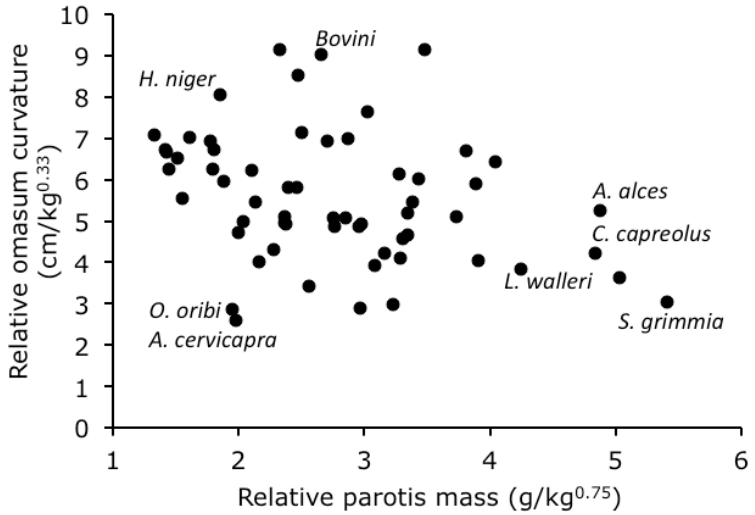
*to whom correspondence should be addressed at mclauss@vetclinics.uzh.ch

Abstract
The omasum is the third forestomach compartment of pecoran ruminants. It is assumed that the re-absorption of fluid present in the forestomach digesta (that facilitates particle sorting, digestion, and harvest of microbes) is its main function, so that less diluted digesta is submitted to enzymatic digestion in the lower digestive tract. Here, we evaluate measures of omasum size (representing 84 ruminant species in the largest dataset) against body mass and proxies of the natural diet (%grass) or forestomach physiology (fluid throughput), using phylogenetically controlled models. The origin of specimens (free-ranging or captive) did not have an effect in the dataset. Models with the best support invariably either included %grass or a physiology proxy in addition to body mass. These effects were not necessarily additive (affecting the intercept of the allometric regression), but often indicated a change in the allometric body mass-exponent with diet or physiology. Only models that allowed an influence on the allometric exponent yielded basic exponents compatible with predictions derived from geometry. Species that include more grass in their natural diet, or that have a 'cattle-type' physiology marked by a high forestomach fluid throughput, generally have larger omasa. However, the existence of outliers, as well as the overall data pattern, suggest that this is not an obligatory morphophysiological condition. Circumstantial evidence is presented leading to the hypothesis that the comparatively small and less complex omasa of 'moose-type' species do not necessarily represent an 'original' state, but may be derived from more complex states by ontogenetic reduction and fusion of omasal laminae.

Key words Convergence, Rumination, Digesta washing, Ruminantia, Feeding niche, 'Moose-type', 'Cattle-type'

Highlights

Graphical abstract



Relationship between the relative parotis gland mass and the relative omasum size (measured as curvature length). Note that the current interpretation of salivary gland size links larger glands to constraints on salivary volume output, i.e. relatively smaller glands are thought to achieve a higher saliva flow, hence making a larger omasum for fluid re-absorption adaptive. Outliers with very small omasa (oribi and blackbuck) and with very large omasa (the Bovini) indicate that the overall pattern is common but not obligatory.

Introduction

The omasum: function and diversity

Functional ruminants - the camelids and the taxonomic ruminants - achieve a degree of ingesta particle size reduction unequalled by other herbivores of similar size (Fritz et al. 2009a; Clauss et al. 2015). This is possible due to a sorting mechanism in their forestomachs that selectively retains larger particles and re-submits them via regurgitation to repeated mastication, i.e. rumination (Dittmann et al. 2015b). The sorting mechanism is based on the differential buoyancy of small and large particles (Sutherland 1988; Lechner-Doll et al. 1991), and requires an organ with comparatively liquid contents, in which separation due to flotation and sedimentation can occur. In camelids, this organ is called the C2 (Pérez et al. 2016); in ruminants, it is the reticulum (Clauss et al. 2010a). The fluid-based mechanism poses the problem that theoretically, together with the fine particles, a large amount of fluid will pass into the lower digestive tract that will then dilute digestive enzymes.

Taxonomic ruminants have evolved an anatomical structure whose primary function is considered to be the removal of that liquid before the digesta reaches the sites of gastric acid and enzyme secretion - the omasum (Clauss and Hofmann 2014). Based on the fact that tragulids - the most 'primitive' ruminants - do not have an omasum, this organ has been interpreted as a 'key innovation' that facilitated the replacement of a once more diverse tragulid fauna by more advanced ruminants, the 'crown pecora' (Clauss and Rössner 2014). Differences in the size, shape and structure of the omasum between ruminant species have been described for a very long time (Garrod 1877; Langer 1973), and the comparative work of Hofmann put this variation in a context of feeding adaptations, with grazers generally having larger omasa than browsers (Hofmann 1969, 1973, 1988; Langer 1988; Clauss et al. 2006a). However, differences linked to phylogeny rather than feeding type were also mentioned early on, as when Hofmann (1969) observed that mixed-feeding gazelles (*Gazella*, *Eudorcas* and *Nanger* spp.) in general had smaller omasa for their body size than browsing duikers

(*Sylvicapra grimmia* and *Cephalophus* spp.) or dikdiks (*Madoqua* spp.), or when Clauss and Hofmann (2014) stated that Bovini and muskoxen (*Ovibos moschatus*) in general are distinct from other ruminants in terms of an exceptionally large omasum. Nevertheless, a functional measure of omasum size, the laminar surface area, correlated significantly with the percentage of grass in the natural diet in a dataset of 34 species, supporting the interpretation that grazing ruminants in general have larger omasa (Clauss et al. 2006a).

In the attempt to further advance the comparison of ruminant feeding types (grouped by the botanical description of their diet - browse vs. grass) and their digestive physiology, ruminants were classified into two broad physiological categories (Clauss et al. 2010b). One is the 'moose-type', with homogenous rumen contents and a low rumen fluid throughput (hence, theoretically, able to function optimally without large omasa). The other is the 'cattle-type', with stratified rumen contents and a high rumen fluid throughput (hence, theoretically, requiring larger omasa for optimal efficiency). 'Moose-type' ruminants are typically strict browsers, whereas 'cattle-type' ruminants can be mixed feeders or grazers (Codron and Clauss 2010). Amongst other characteristics, the digestion types can be classified using the homogeneity of the ruminal papillation (Clauss et al. 2009c), and by the difference in the retention time of particles and fluids in the forestomach (Dittmann et al. 2015a). It has recently been speculated that the 'cattle-type' digestive physiology is not directly aimed at a characteristic of grass forage, but that it optimises the harvest of microbes from the forestomach by an increased washing of forestomach contents by fluid, which removes microbes into the lower digestive tract (Clauss and Hummel 2017). In this concept, larger omasa would not strictly reflect an adaptation to a grass diet, but an adaptation to a high degree of microbial harvest. This concept could be more easily reconciled with the observation that the largest omasa occur in the bovid tribe Bovini but not in the strictest grazing species (Clauss and Hofmann 2014).

Allometric investigations: how to test for an influence on scaling

A fundamental question in the assessment of allometric relationships is which factors cause animal groups to vary in a measurement. Allometric equations are typically in the form of

$y = a\ BM^b$ [or $\log y = \log a + b \log BM$] (I)

where BM is body mass, *b* represents the scaling with body mass, and *a* is a measurement-specific factor. Often, it is assumed by default that a difference between groups is evident in a change of the intercept of the allometric equation:

$y = a\ BM^b\ c\ factor$ [or $\log y = \log a + b \log BM + c\ factor$] (II)

where *c* represents the influence of the factor in question (for example, percent grass in the natural diet), and *a* the intercept when the factor is zero. An implicit - although maybe not always explicitly stated - test of whether this reflects how the factor influences the allometric relationship is whether the magnitude of *b* corresponds to general geometric concepts. Based on simple geometry, linear measurements should scale to $BM^{0.33}$, area/surface measurements should scale to $BM^{0.67}$, and volume or mass measurements should scale linearly, i.e. to $BM^{1.00}$ (Calder 1996). For example, linear measurements of the reticulum or the tongue of ruminants scaled in this fashion (Clauss et al. 2010a; Meier et al. 2016).

Another theoretical possibility how a factor could influence a scaling relationship is by an effect on the exponent *b*; this might be particularly the case in situations where the factor in question is not distributed homogeneously across the measurement range. This would result in a scaling in the form of

$y = a\ BM^{(d + c\ factor)}$ [or $\log y = \log a + d \log BM + c\ factor \log BM$] (IIIa)

where *d* is the geometric scaling exponent and *c* a constant weighting the effect of the factor. It is evident that this represents a model where a significant interaction between BM and the factor is expected.

If such exponent-influencing scaling was to occur, we would expect models I and II to yield a value for *b* different from the one expected by geometric scaling, but model III to yield

a value for *d* that is close to geometric scaling. Additionally, model III should account for a higher proportion of the total variance in the data.

Aims of this study

Here, we used a data collection on the anatomy of the ruminant omasum from various sources, including previously unpublished material, to investigate whether variation among ruminant species could (i) be explained by their natural diet, while (ii) hypothesizing that proxies for their digestive physiology would explain this variation to a higher degree than the natural diet itself.

In concrete terms, we expected that species with a higher percentage of grass in their natural diet have larger omasa, that species with a distinct intraruminal papillation gradient have larger omasa, and that species with a more distinct difference in particle vs. fluid retention in the reticulorumen have larger omasa (i.e., Type II and Type III models that include a covariable would yield a better data fit than Type I models that only account for body mass). Among the Type II and Type III models, we expected that proxies for physiology (intraruminal papillation gradient, the ratio of particle vs. fluid retention) would lead to a better data fit than the percentage of grass in the natural diet. In testing for these allometric relationships, we explored how phylogenetic affiliation, and the assumed mathematical influence of the respective covariables on the allometric exponent (Type II vs. Type III), influenced data fit and the deviation of the allometric exponent from basic geometry.

Methods

Anatomical data sources

Anatomical measurements were either taken from existing publications (Ledger and Smith 1964; Hofmann 1973; Lauwers 1973; Nagy and Regelin 1975; Hofmann et al. 1976; Geiger et al. 1977; Church EC 1978; McSweeney 1988; Takatsuki 1988; Holtenius and Björnhag 1989;

Werner 1990; Pfeiffer 1993; Sibbald and Milne 1993; Stafford and Stafford 1993; Hofmann et al. 1995; Holand and Staaland 1995; Reissig 1995; Staaland et al. 1997; Li et al. 2000; Mathiesen et al. 2000; Clauss et al. 2005; Clauss et al. 2006a; Clauss et al. 2006c; Jiang et al. 2006; Clauss et al. 2009d; Booyse and Dehority 2012; Pérez and Ungerfeld 2012; Pérez and Vazquez 2012; Jerbi and Pérez 2013; Pérez et al. 2015; Bonin et al. 2016; Jerbi et al. 2016; Sauer et al. 2016a; Sauer et al. 2016b; Sauer et al. 2017; Tahas et al. 2017) or from previously unpublished observations during dissections performed by both senior authors. The data are given in the electronic supplements. Animals originated from the wild (e.g., from hunting operations) or from captivity (mainly, from zoological collections).

Measurements

Data for body mass (BM) was taken from the original literature sources, where it did not always reflect the measured BM of the investigated specimens, but included estimates; for unpublished data, BM reflects actual weighing of the investigated specimens. The following anatomical measurements were taken (for a visualization, cf. Fig. 2 in Sauer et al. 2016b): The curvature, length and height of the omasum (in cm), the number of first order and second order leaves and the total number of leaves (n), the omasal laminar surface area (in cm^2), the mass of the empty omasum and of its contents (in g). All measurements were taken after removal of adipose or connective tissue (e.g. between the omasum and the *Atrium ruminis*) and lymph nodes.

The linear measurement of curvature is taken as the (straight) distance between the connection of the omasum and the reticulum along the largest possible curvature to the connection of the omasum with the abomasum. It is taken with a soft measuring tape and reflects the shape of the organ, and is curved in one and straight in the other dimension. Measurements of length and height are taken with the forestomach complex lying on its left side. They do not follow the organ contour and are taken with a rigid measuring stick or

callipers. Because these linear measures are the easiest ones to take, requiring no further dissection after exenteration and removal of adnexa, they represent the largest datasets in this collection.

Definitions for the ascription of omasal leaves to a certain order vary in the literature. Mostly, 'order' is referred to as a relative position, with the largest leaves in the respective omasum being called 'first order', the next largest leaves 'second order' and so on. These leaves are staggered in alternating order 2-1-2 ... Especially as the base of the leaves approaches the omasal canal, leaves can become small, and ascription to an order may not reflect size but only consistency of the alternating order. Therefore, first and second order leaves are often of a similar number. Smaller leaves of third and fourth order are usually inserted between the other orders in the fashion of 3-2-3-1-3-2-3-1-3 ... , or as 4-3-4-2-4-3-4-1-4-3-4-2-4-3-4-1-4-3-4 ... In these cases, not every third or fourth order leaf is necessarily present, but may be either missing completely or only be present as a ridge of papillae. In animals with three or more leaf orders, as the base of the leaves comes close to the omasal canal, it is often not possible to decide whether a leaf represents a small third order leaf or a second order leaf (with the third order one missing). This introduces a certain subjectivity in the number of second and higher order leaves. This system was generally used by the main data collector of the present study (Hofmann 1969, 1973, 1988), the senior author (Clauss et al. 2006c; Clauss et al. 2009d), and in work supervised by them (Werner 1990; Sauer et al. 2016a; Sauer et al. 2016b; Sauer et al. 2017; Tahas et al. 2017). All data referring to the number of first and second order leaves in the present study were derived in this way. Another approach uses fixed absolute laminar size thresholds for the categorisation of the leaf order that are not adjusted for body mass (Stafford and Stafford 1993). In that system, smaller ruminants may not have any omasal leaves of a first or second order, because their omasum is generally not of a sufficient absolute size to fall into those categories, but is only ascribed to have third and fourth order leaves. Because the two systems are not compatible, data on

leaves of a certain order from Stafford and Stafford (1993) were not used in the present study. However, data on the total number of leaves, irrespective of their order, was included.

The omasal laminar surface area is measured by planimetry of all omasal leaves (multiplying the sum of all individual laminar surface measurements by two, to account for both sides of the leaves) after dissecting them out of the organ (Stafford and Stafford 1993; Clauss et al. 2006a; Sauer et al. 2016b). As this dissection requires considerable time, especially in larger species with leaves of third, fourth (and sometimes fifth) order, the data collection comprises fewer species for this measurement.

Organ tissue mass is measured by weighing after emptying the organ by carefully rinsing between the individual leaves and allowing the water to drip off or squeezing it off the organ. Organ content mass is measured as the difference between the unopened, full organ mass and its tissue mass.

Averages for measurements were calculated for free-ranging and zoo specimens separately. Not all measurements were taken in all specimens. Therefore, BM is not constant across measurements for a species, but reflects the actual average of those specimens in which the respective measure was taken. Finally, a dataset with the maximum number of species was composed, using the data of free-ranging animals as a basis, and adding those species for which only data from captive specimens were available.

Biological data

The anatomical data was evaluated using three additional datasets reflecting the natural diet, and the digestive physiology. The natural diet is typically described as the percentage of grass in the natural diet (%grass) (Clauss et al. 2008b) and was available for all species investigated (Gagnon and Chew 2000; Clauss et al. 2010a; Clauss et al. 2011; Müller et al. 2011a; Serbent et al. 2011; Zerbe et al. 2012; Dittmann et al. 2015a; Akbari et al. 2016; Meier et al. 2016;

Rduch 2016). In order to achieve more convenient parameter estimates for the natural diet, we expressed %grass in this study as the proportion of grass (i.e., ranging from 0-1 rather than from 0-100).

Digestive physiology was represented by two measurements. The surface enlargement factor (SEF) ratio of the dorsal rumen as a percentage of the SEF in the *Atrium ruminis* (Clauss et al. 2009c), is a proxy for the stratification of rumen contents, with smaller values indicating animals with a less homogenous intraruminal papillation pattern (a more distinct intraruminal papillation gradient), and hence stratified rumen contents with a higher fluid thoughput. This measure is negatively (but not linearly) related to %grass across ruminant species (Clauss et al. 2009c; Codron and Clauss 2010). In order to make models including this factor more comparable to models involving the proportion of grass in the natural diet, or the selectivity factor in the reticulorumen (see below), the relative SEF (rSEF) was expressed as rSEF = 1-(SEFratio/100) so that we expect it to be positively related to %grass. The reindeer (*Rangifer tarandus*) represents a distinct outlier in this pattern (Codron and Clauss 2010), and rSEF analyses were therefore performed without this outlier; additionally, the blackbuck (*Antilope cervicapra*) was also excluded (see next paragraph).

The selectivity factor in the reticulorumen (SF RR) is the ratio of small particle to fluid retention times, with higher values indicating a higher fluid throughput relative to particle retention (Dittmann et al. 2015a). It is typically positively (but not linearly) related to %grass, where species above a threshold of about 20 % grass in the natural diet have higher SF RR (Dittmann et al. 2015a), and is negatively related to the intraruminal papillation gradient (Tahas et al. 2017). The blackbuck (*Antilope cervicapra*) has been described as an outlier in terms of omasum anatomy, with a very high SF RR yet an unexpectedly small omasum (Hummel et al. 2015; Sauer et al. 2016a). The rSEF and SF RR analyses were therefore performed without this outlier. The rSEF and the SF RR were available for different numbers

of species, and evaluations including these measures therefore had to be performed on smaller data subsets.

Allometric models and geometric effects

Based on simple geometry, we expected the linear measurements (omasum curvature, length, height) to scale to $BM^{0.33}$, the omasal laminar surface area to scale to $BM^{0.67}$, and organ tissue and organ content mass to scale to $BM^{1.00}$ (Calder 1996). With respect to the data at hand, it appears unclear what scaling to expect for the number of omasal leaves. An exploratory analysis revealed that the total number of omasal leaves scales with omasal curvature to an exponent that includes linearity in its 95% confidence interval (Fig. S1), suggesting that the number of leaves that can be inserted in the omasum wall is directly proportional to a linear measurement of that wall. Therefore, the total number of omasal leaves is tentatively expected to scale, as a linear measurement, to $BM^{0.33}$.

In the log-transformed version of equation IIIa, an interaction term between the factor in question and body mass is implied. For statistical purposes, to account for variance explained by it, the factor interacting with body mass needs to be retained also as a covariate in the model, so that the log-transformed version of the analysis is

$$\log y = \log a + d \log BM + e \text{ factor} + c \text{ factor } \log BM \qquad \text{(IIIb)}$$

Statistics and data presentation

The effect of animal origin (free-ranging vs captive) was assessed in pairs of species where measurements were available for both origins, first by paired t-tests, and second by General Linear Models (using log-transformed data; confirming normal distribution of residuals) that link an anatomical measure to body mass and include origin as a co-factor. Additionally, the effect of origin was assessed using all available data for free-ranging and captive specimens (i.e. allowing species to occur once or twice in the dataset) in General Linear Models, using

origin as a cofactor. Nonparametric correlations (Spearman's ρ) were used to test associations between body mass, %grass, rSEF and SF RR.

Allometric relationships between BM and omasum anatomy were evaluated using linear regressions of log-transformed data, with BM as the covariate and each anatomical measure as the dependent variable (equation I). For each anatomical measure, the influence of diet (proportion of grass in species' natural diets) and rumen physiology (rSEF and SF RR, respectively) was tested for by introducing each of these as covariates, in turn, to the regressions using General Least Squares Regressions (GLS). These additional covariates represent the factors in equations II (without interaction term) and IIIb (with interaction term), respectively. Relative goodness-of-fit of each model was then compared using the small sample-corrected Akaike's Information Criterion (AIC_c), following guidelines that models with $\Delta AIC_c < 2$ are considered to be best-supported by our data (Burnham and Anderson 2001, 2002). ΔAIC_c is calculated as the difference between the AIC_c of a candidate model and the minimum AIC_c score in the whole set. The rationale behind this approach is that because the AIC_c score penalizes for the addition of parameters, we only consider factors other than BM to have a significant influence on the data in cases where diet or physiology contribute sufficiently to the whole model to warrant inclusion of the additional parameter. In this way, we ranked the goodness-of-fit of models in which BM was the only covariate (Type I), where diet or physiology was a covariate influencing the intercept of the allometry (Type II), and where diet or physiology influenced the allometric scaling exponent (Type III).

These procedures were repeated for the full datasets (for which the proportion of grass in diet is the only additional covariate), and reduced datasets for which rSEF (excluding reindeer and blackbuck) and SF RR (excluding blackbuck) data are available (see above). To account for any phylogenetic influence on these allometries, we repeated the above analyses using Phylogenetic Least Squares Regressions (PGLS). For this approach, we used a mammalian supertree (Fritz et al. 2009b), pruned to include the relevant taxa in our dataset,

and subsets. The tree was then correlated with our dataset in PGLS, and strength of the phylogenetic signal (λ) estimated by maximum likelihood. All analyses were carried out in R v 3.3.2 (R_Core_Team 2015), with the package 'nlme' (Pinheiro et al. 2011) for GLS and the package 'caper' (Orme et al. 2013) for PGLS analyses.

For visualisation, relative omasum measurements (per $kg^{0.33}$ or $kg^{0.67}$ or $kg^{1.0}$, depending on the respective measurement) were plotted against %grass, rSEF or SF RR.

Results

Comparison between free-ranging and zoo specimens

Using the (log-transformed) dataset for which the largest number of species pairs existed in which both free-ranging and captive specimens had been measured (curvature, n = 15 species pairs), there was no significant difference in body mass (176 ±214 kg in the wild vs. 172 ±214 kg in captivity, paired t-test $P = 0.530$), but the curvature was longer in the wild (30.6 ±18.8 cm vs. 27.0 ±19.9 cm in captivity, $P = 0.006$). In contrast, using the three largest (log-transformed) datasets for which such species pairs existed (n = 15 species pairs for curvature, n = 12 species pairs for length, n = 13 species pairs for height; Fig. S2) in GLMs with the measurement as the dependent variable, body mass as the independent variable, and origin (wild/captivity) as a cofactor, neither origin (curvature $P = 0.134$, length $P = 0.079$, height $P = 0.283$) nor the body mass x origin interaction ($P = 0.176$ to 0.421) were significant. Using all available data for free-ranging and captive specimens (i.e. allowing species to occur once or twice in the dataset) for similar GLMs for all measurements did not yield a significant effect of origin ($P = 0.129$ to 0.907) or body mass x origin interaction ($P = 0.273$ to 0.982) except for omasum length, where both origin ($P < 0.001$) and the body mass x origin interaction ($P = 0.009$) were significant (Fig. S3). Given the prevailing lack of effect of origin in the GLMs, we considered it adequate to continue our analyses with a dataset comprising of

species averages for free-ranging individuals that was supplemented, for species that were only investigated in specimens from captivity, by species averages for captive individuals.

Data visualisation

Whereas there was a significant correlation between body mass and %grass (ρ = 0.42, P < 0.001) and body mass and rSEF (ρ = 0.47, P = 0.001; indicating a decrease of the SEFratio with body mass), there was no such correlation with SF RR in the dataset (ρ = 0.27, P = 0.189; Fig. S4). As described previously, the SEFratio decreased, and SF RR increased, with increasing %grass (ρ = -0.79, P < 0.001 and ρ = 0.53, P = 0.006, respectively; Fig. S5) (Clauss et al. 2009c; Dittmann et al. 2015a). There was also a negative correlation between the SEFratio and SF RR (ρ = -0.99, P = 0.004; Fig. S6) as described previously (Tahas et al. 2017).

We display the three datasets (for species for which %grass, rSEF and SF RR were available, respectively) for the omasum measurement with the largest number of entries of our study (the omasal curvature) in Fig. 1. The data for the other omasum measurements are displayed as Fig. S7-S12. As expected, there were evident patterns with an increase in all omasum measurements with body mass. Relative omasum measurements tended to show a moderate increase with %grass, with a strong effect of the respective dataset, as exemplified in Fig. 1: Whereas the relationship between %grass and the relative omasum curvature was clearly visible in the rSEF-dataset (Fig. 1B), it was less distinct in the %grass- (Fig. 1A) or the SF RR-dataset (Fig. 1C). The only exceptions to the pattern with %grass were the two omasum measures for which the lowest number of species had entries in our study, the omasum tissue and the omasum content mass (Fig. S11 and S12). Most relative omasum measurements tended to show a decrease with a more stratified intraruminal papillation pattern, and an increase with SF RR; again, these patterns were not evident for the two

omasum measures for which the lowest number of species had entries in our study, the omasum tissue and the omasum content mass (Fig. S11 and S12).

Allometric scaling and the natural diet (complete datasets)

While there was a significant phylogenetic signal λ for the largest data subset (omasum curvature) and several other subsets, this was not the case for the total number of leaves and the omasal leaf surface. Generally, PGLS results did not differ qualitatively from GLS results.

In simple allometric analyses of all omasum measurements (Type I models), the resulting exponents *b* were always larger than expected from geometry in GLS, and included the expected geometric exponent in the 95% CI in PGLS only for organ mass, content mass, and the total number of leaves (Table 1). Type I models were among the best-supported in 3 out of 9 GLS and 4 out of 9 PGLS analyses. Similarly, Type II models including %grass were among the best-supported in 4 GLS and 3 PGLS analyses. In contrast, Type III models including %grass were among the best-supported in 8 GLS and 7 PGLS analyses, making this model type the most 'successful' for this dataset. In all cases, except for the laminal surface area in both GLS and PGLS, Type III models resulted in lower scaling exponents than simple Type I allometries, and included geometric scaling in their 95% confidence intervals. In contrast, Type II models did not change the scaling exponents as compared to simple Type I allometries, except for one case in GLS (total number of leaves) and one case in PGLS (omasum height).

Allometric scaling, natural diet and intraruminal papillation (reduced datasets)

In these reduced datasets, there was a strong phylogenetic signal λ only in the curvature subset, but not in most other subsets. Irrespective of whether the λ was significantly different from zero or not, the PGLS approach generally did not yield a different model ranking than the GLS approach.

In simple allometric analyses of all omasum measurements (Type I models), the resulting exponents *b* were larger than expected from geometry in GLS except for number of leaves, organ and content mass, and included the expected geometric exponent in the 95% CI in PGLS additionally for omasum length (Table 2). Type I models were among the best-supported in 3 out of 9 GLS and 3 out of 9 PGLS analyses. Type II models including either %grass or rSEF were among the best-supported in 7 GLS (only one for rSEF) and 8 PGLS (only two for rSEF) analyses. Similarly, Type III models including either %grass or rSEF were among the best-supported in 6 GLS and 7 PGLS analyses. rSEF achieved a better support than %grass in one of these cases in both GLS and PGLS (as opposed to 7 cases where %grass achieved better support, and one with equal support for both). In all cases, except for the total number of leaves, organ and contents mass in GLS and additionally for length in PGLS, Type III models resulted in lower scaling exponents than simple Type I allometries, and also included geometric scaling in their 95% confidence intervals. In contrast, Type II models did not change the scaling exponents as compared to simple Type I allometries. Also, results for this dataset represent the only occasion in which exponents for laminar surface area included geometric scaling.

Allometric scaling, natural diet, and fluid throughput (reduced datasets)

In these even further reduced datasets, there was a significant phylogenetic signal λ for the curvature and height subsets. Irrespective of whether the λ was significantly different from zero or not, the PGLS approach again did not yield a generally different model ranking than the GLS approach.

In simple allometric analyses of all omasum measurements (Type I models), the resulting exponents *b* were larger than expected from geometry in both GLS and PGLS except for omasum height, number of leaves, organ and content mass (Table 3). Type I

models were among the best-supported in 5 out of 9 GLS and 4 out of 9 PGLS analyses. Type II models including either %grass or the SF RR were among the best-supported in all 9 GLS (either SF RR only, or both SF RR as well as %grass) and all 9 PGLS (2 times SF RR only, 2 times %grass only) analyses. Type III models including either %grass or SF RR were among the best-supported in 3 GLS and 2 PGLS analyses. Differences in the 95% CI of the exponent were more rare for this even more limited dataset. Type III models achieved the expected exponents in 3 analyses in GLS and 3 in PGLS where Type I models did not.

Discussion

The present study yields statistical support for the hypothesis that omasum size across ruminant species is better explained when including the natural diet, or a proxy of forestomach physiology, than by body mass alone; that the effect of the diet is in the direction originally hypothesized by Hofmann (1973, 1988, 1989); and that the effects of other physiological proxies also match, in their direction, recent narratives about comparative ruminant forestomach physiology (Clauss and Hofmann 2014; Clauss and Hummel 2017). However, in doing so, the study also draws attention to the fact that the expected relationships show a high degree of data scatter that defies an interpretation of obligatory adaptations. It also raises the issue of the mathematical approach to evaluate factors suspected to influence an allometric relationship.

Limitations

The most serious limitation of our study refers to the consistency of data collection, which depends on measurements taken by various investigators, even within the same investigators over long periods of time, on different numbers of specimens, and which combines species-specific data that were hardly ever consistently recorded on the same specimens. For example, information on the natural diet is typically not derived from the specimens submitted to anatomical investigation. Additionally, the use of body mass as a proxy to correct for effects

of body size, although widely accepted, most likely introduces measurement error whose effect is difficult to gauge: body mass will vary much more with current nutritional status, due to variation in adipose and muscle tissue, than many organs.

Considering the interplay of measurements related to forestomach physiology - the intraruminal papillation gradient, the rumen contents stratification, and the ratio of particle vs. fluid retention, and omasum size, there is only a single species in the whole dataset (*Addax nasomaculatus*) for which all these measures were taken in the same individuals (Hummel et al. 2008; Clauss et al. 2009b; Tahas et al. 2017). Ideally, comparative anatomical data should be generated by a team of investigators within a defined period of time, under standardized conditions (in the habitat considered the typical for the species, during a period of either optimal or limiting resource availability), on a consistent number of specimens of each species considered, recording not only body mass but less condition-dependent proxies for body size. Such an approach is feasible for concise questions limited to species of a specific region (e.g. Snelling et al. 2018), but is much more difficult to achieve on a global level.

While it has been shown that diet can have an effect on omasum size (Lauwers 1973; Bailey 1986; reviewed in Tahas et al. 2017), no consistent effect of the origin of the specimens, as described as the dichotomy between free-ranging and captive individuals, was evident in our dataset. Inspecting plots in which each species is represented by specimens from both origins (Fig. S2) indicates that a difference between the origins was not consistently in the same direction. Similarly, inspecting plots that included origin means of all available data does not consistently indicate higher values in animals of any one origin (Fig. S3). The most likely reason for these inconsistencies is that diets in captivity are not uniform across species in their resemblance to the natural diet. Also, it has been previously speculated that differences in natural diet between individuals of the same species might account for intraspecies variation in omasum anatomy (Lentle et al. 1998).

Effect of phylogeny

The fact that the phylogenetic signal was significant, in particular for the largest dataset on omasum curvature and %grass, corroborates the impression that different ruminant groups are characterized by general differences in their omasum size that cannot be explained by their natural diet alone. As stated previously, Bovini and muskoxen have particularly large omasa, whereas gazelle species have particularly small omasa (Fig. 1). The fact that a significant phylogenetic signal is found even in models that include two morphophysiological measures (i.e., omasum size proxies and proxies for either the intraruminal papillation gradient or the rumen fluid throughput), and even although known evident outliers were not included in the analysis, indicates that covariation in these morphophysiological traits is not consistent across taxa. These observation leads to the conclusion that different ruminant groups have evolved different (combinations of) solutions to digestive processes and dietary niches, even though a general trend emerges when assessing species across a certain taxonomic and ecological range (see below).

Mathematical approach to testing influence on allometries

We compared models that treat an influence factor as a mathematical addition, or in other words, a change in the intercept in a regression model (Type II), with models that treat the influence factor as a modifier of the allometric exponent, or in other words, a change in the slope of the regression model (Type III). In the largest dataset (that only considered %grass as a covariable), Type III models had most often the best support. In particular, for the measure for which the largest number of entries in the dataset existed, the omasum curvature, the difference in data fit between the Type III and both the Type I and Type II model was substantial (Table 1). The biological interpretation is a shift of a basic exponent depending on the natural diet.

The biological justification for considering Type III models is that in our analyses, these models generally led to allometric exponents that would be expected based on simple geometric rules, in particular a scaling to $BM^{0.33}$ for linear measurements. However, irrespective of the data fit, one should not immediately accept this result as a description of a biological phenomenon. Rather, one should consider the data pattern, for example by plotting the data and the resulting models. Doing this for the largest dataset, the omasum curvature, gives a plausible scenario for the large ruminant species (Fig. 2A), but the variation in the low body mass range of 2-20 kg is not explained well (Fig. 2B). Arguably, the latter is a body size range where variation in the natural diet is low (Fig. S4), and where differences in the relative position of species are more prone to measurement error, due to small organ size, than at larger body sizes. Formally, Type III models represent significant interactions with different slopes between species of a fixed %grass in the natural diet in log-log plots. In other words, if species would have been classified in terms of their natural diet not by a continuous variable (%grass), but by categories (browser/grazer), the interaction would have represented a formal obstacle to statistical comparison (Demment and Longhurst 1987; Clauss et al. 2002). This is not the case in our approach with a continuous diet proxy.

But nevertheless, an important aspect of different scaling slopes for different data subsets is whether the point of intersection of the regression lines represents the origin of deviation (i.e., from this point onwards, the regression lines deviate due to different slopes), or whether it represents a crossing point that separates two parts of the dataset where the relative positions of the respective regression lines change (Stillwell et al. 2016). While the former scenario offers an intuitive explanation (from a certain point onwards, one group shows a steeper scaling than the other), the latter scenario typically represents an explanatory challenge. If one would, for example, prolong the Type III regression lines in Fig. 2B for species with 100% grass in the natural diet into the lowest body size range (where such species are factually absent), this model, which had the best fit, would predict smaller omasa

for grazing species than for species consuming more browse. No potential functional reason for such a pattern has been put forward to date, and we recommend that our result is not extrapolated in this manner.

Forestomach physiology and diet niche

Instead, there is theoretical background for a scenario in which 'cattle-type' ruminants or mixed feeders/grazers have larger omasa (Clauss and Hofmann 2014). First, we assume that there is an integration of forestomach function with respect to fluid throughput, which differs between ruminant species and separates 'moose-type' from 'cattle-type' ruminants (Clauss et al. 2010b). A high relative degree of fluid throughput through the reticulorumen is measured as a high SF RR (Dittmann et al. 2015a). This leads to a distinct stratification of rumen contents, measured as the difference in fluid concentration of dorsal and ventral rumen contents (Fig. 3A). Such a stratification of rumen contents is linked to an intraruminal papillation gradient, with species with a low degree of stratification having a more even ruminal papillation (Fig. 3B). Correspondingly, a high SF RR is linked to a distinct papillation gradient (Fig. 3C). A major task of the omasum is to remove excessive fluid from the digesta, as occurring at high fluid throughput, and it is a reasonable assumption that larger omasa, with their larger absorptive surface, can absorb more fluid per unit of digesta moving through them. Therefore, relative omasum size tends to increase with increasing SF RR (Fig. 3D), with a more distinct rumen contents stratification (Fig. 3E), and with a more distinct intraruminal papillation gradient (Fig. 3F). The data available for the different combinations supports this interpretation. A certain degree of data scatter may be attributable to measurement discrepancies and the fact that individual measures were taken from different individuals within a species. However, the data and the outliers also indicate that different ruminant species follow these patterns at varying degrees, making this integrated set of characteristics a predominant but not an obligatory adaptation across ruminant species.

Secondly, we assume a general benefit of a high fluid thoughput/digesta washing in the form of a more intensive harvest of microbes from the rumen contents (Müller et al. 2011b; Hummel et al. 2015; Clauss and Hummel 2017). In theory, all ruminants would benefit from this effect, which may explain why the majority of ruminant species investigated so far shows 'cattle-type' adaptations for a high fluid throughput (Dittmann et al. 2015a). While specific adaptations of the oral processing apparatus to browse or grass diets can be demonstrated and explained in terms of biomechanics (Gordon and Illius 1988; Archer and Sanson 2002; Clauss et al. 2008a; Heywood 2010; Kaiser et al. 2010; Meier et al. 2016), forestomach morphophysiology does not seem to follow a strict dietary gradient regardless of broad interspecific patterns. Rather, an increased range of morphophysiological options appears to be used above a threshold of approximately 20% of grass in the natural diet (Hofmann et al. 2008; Clauss et al. 2010a; Dittmann et al. 2015a). For this reason, we had expected that physiological proxies of fluid throughput would yield a better data fit than %grass; while this seemed somehow true for SF RR, it was not for rSEF, which indicates that, as illustrated in Fig. 2 and Fig. S5, and exemplified prominently by the outlier position of the blackbuck, morphophysiological characteristics are not necessarily more strictly integrated with each other than with the natural diet.

Thirdly, a link between fluid throughput and diet can be construed from a possible defence strategy against secondary plant metabolites (which are more prominent in browse than in grasses) by salivary proteins. This strategy putatively requires larger salivary glands in animals that use it, and is thought to constrain saliva production rate and hence the amount of fluid that can be put through the forestomach system (Hofmann et al. 2008). Many browsing ruminants therefore show characteristics of a low-throughput system. Note that larger salivary glands are not linked to higher amounts of saliva in this scenario, but on the opposite to lower amounts of a more proteinaceous saliva. Their size is linked to defensive protein production, which leads to more viscous saliva (Clauss et al. 2009a; Clauss et al. 2009b; Lechner et al.

2010). By contrast, without the necessity to produce these salivary proteins, smaller salivary glands can putatively produce copious amounts of low-viscosity fluid (Hofmann et al. 2008). If this reasoning were correct, we would expect species with relatively large salivary glands to require relatively small omasa, because a lower amount of fluid needs to be absorbed (Clauss et al. 2006b). Plotting relative parotis gland mass from Hofmann et al. (2008) and Tahas et al. (2017) against relative omasum size from the present study for species present in both datasets apparently supports this concept, with again Bovini as outliers with large omasa for their not-so-small salivary glands, and both the blackbuck and the oribi (*Ourebia oribi*) as outliers with small omasa for their small salivary glands (Fig. 4).

Omasum development

The origins of differences in omasum morphology must lie either in the embryologic *anlage*, or in ontogenetic development. In various ruminant species, ridges along omasal leaves have been sporadically mentioned or documented by photographs, as in Hofmann (1973) for dikdiks (*Madoqua* spp.), lesser kudu (*Tragelaphus imberbis*), reedbuck (*Redunca redunca*), and kob (*Kobus kob*), or by Yamamoto et al. (1994) for cattle and sheep. The senior author has observed such structures in moose (*Alces alces*), bison (*Bison bison*), mouflon (*Ovis ammon musimon*) and roe deer (*Capreolus capreolus*). To our knowledge, however, no list exists of species in which such structures do or do not occur. Examples of first order leaves of a giraffe (*Giraffa camelopardalis*) with two of such ridges are displayed in Fig. 5. Based on the visual appearance, it is tempting to speculate that these structures represent the result of a fusion of higher-order leaves with the lower-order leaf. Differences in apparent omasal leaf thickness that have been mentioned repeatedly, without actual quantification, support this impression. Hofmann (1969) noted that small, less complex omasa often had comparatively thick leaves, and the descriptions of individual species by Hofmann (1973) indicate the same pattern. This impression is evident in comparing omasal leaves of a complex omasum in red

deer (*Cervus elaphus*, with very thin leaves of 4 orders) with that of a more simple omasum in roe deer (with thick leaves of only 2 orders) (Hofmann et al. 1976). A comparison of ontogenetic series of cattle (complex omasa) and giraffe (simpler omasa) indicates more surface per gram omasum tissue in cattle (Fig. 6A), supporting the idea that omasum complexity is linked to thinner structures. Differences in leaf thickness, or in the occurrence of the mentioned ridges, remain to be investigated in a comparative way.

If this view was correct, we would expect that a certain number of leaves is present in the ruminant foetus, and that these leaves either mature into individual, thin leaves (in complex omasa) or are fused into thicker, 'composed' leaves (in less complex omasa). Although a large number of studies investigated the foetal development of the omasum (e.g. Redondo et al. 2011; Garcia et al. 2013), this question has hardly been addressed. Reports on embryological evidence of five omasal leaf orders in sheep (Wardrop 1961) or water buffalo (Osman and Berg 1982), where adult animals are often not described as having leaves of five orders, are in agreement with the hypothesized mechanism. Actually, Becker et al. (1952) and Tiwari and Jamdar (1970) reported for cattle and water buffalo, respectively, that fifth order laminae develop on the side of first order leaves. Considering the dense packing of omasal laminae in foetal ruminants as illustrated by the histological sections of Wardrop (1961), and the fact that omasal leaves often fuse anyhow at the abomasal side of the organ, a fusion of budding leaves on the one hand, or a gradual growth of leaf buds into recognizable leaves during ontogeny on the other hand, does not appear far-fetched. In both cattle (Lauwers 1973) and goats (Fonseca et al. 1998) increasing numbers of omasal leaves with age have been documented, which most likely does not imply the origination of new structures, but growth of existing structures to a recognizable size. The fact that there is an apparent increase in total omasal leaf number with age in the complex omasum of cattle with more higher-order leaves, whereas there seems to be no increase in total omasal leaf number with age in the simpler

omasum of giraffe (Fig. 6B), supports this interpretation. The fate of individual omasal leaves in ontogenetic series offers an interesting area for further studies.

Importantly, the proposed scenario of simpler omasa resulting from an embroylogical and/or developmental modification of a more complex *anlage* into a simpler mature form contradicts the interpretation that the simpler structures represent the evolutionary older ones, but explain characteristics of 'moose-type' ruminants / strict browsers as derived adaptations. This is in line with different studies that suggested that mixed feeding, not browsing, is the most likely ancestral feeding niche of modern ruminants (Codron et al. 2008; DeMiguel et al. 2008; Cantalapiedra et al. 2014; Cerling et al. 2015). It has been suggested earlier for the morphology of another forestomach structure of ruminants, the reticulum, and in particular the height of its crests, that the state in many browsing species can also be more easily conceptualized as a derived rather than an ancestral condition (Clauss et al. 2008b; Clauss et al. 2010a).

The higher number of leaves (that all can increase in size) may be the reason why during ontogeny, the omasal leaf surface of cattle has a different growth trajectory than that of giraffe or moose (Fig. 6C). Although the omasa of these species apparently start at comparable surface areas in neonates and juveniles, cattle achieve the highest surface area for their body mass in our entire dataset. Notably, young cattle or giraffe have smaller omasal surface areas than adults of smaller ruminant species at comparable body mass (Fig. 6C), indicating that the increase in omasal surface area during ontogenetic maturation is disproportional with body mass, i.e. with positive allometry. Positive allometric growth for digestive tract organs has repeatedly been documented in ruminants, in particular during the pre-weaning stage (Bailey 1986). The surface area data for both cattle and giraffe show a somewhat corresponding pattern, with a shallower scaling within the older animals only (Sauer et al. 2016b) as compared to the scaling when the newborns and, in the case of cattle, the animals below 200 kg are included (Fig. 6C). The differences in growth patterns must be

the cause of the observed variation in ruminant omasum morphology, and the underlying causes remain to be elucidated.

Conclusion and outlook

The omasum has been termed the most enigmatic of the ruminant stomach compartments (Hofmann 1969), and a variety of functions have been speculatively ascribed to this organ (reviewed in Clauss et al. 2006a). In an integrated view of forestomach physiology, the omasum appears linked to other measures of forestomach fluid throughput (Fig. 3D-F) and salivary gland size (Fig. 4), supporting the interpretation of fluid re-absorption as major function of this organ, and the fact that the majority of ruminant species are aligned in these patterns suggest adaptive value. On the other hand, outliers exist with particularly small omasa, such as the oribi (Hofmann 1973) and the blackbuck (Sauer et al. 2016a), and the tragulids completely lack an omasum (Langer 1973). Additionally, the fact that specimens of domestic ruminants whose omasum was partially surgically removed or circumvented can survive (Trautmann and Schmitt 1935; Hamada 1973) proves that a functional omasum is not an obligatory necessity for a ruminant organism, even if the low number of species with no or exceptionally small omasa - and the historical decline in tragulids in the fossil record (Clauss and Rössner 2014) - allows a narrative where a functional omasum represents a certain evolutionary advantage. Whether the particularly large omasa of Bovini represent an additional escalation (sensu Vermeij 2013), with a morphophysiology tuned to maximizing the effects of digesta washing by an exceptionally high fluid throughput through the forestomach (as hypothesized by Clauss et al. 2010b), remains to be fully explored. With its distinctive anatomy and peculiar growth characteristics, the omasum represents a promising area of embryological and ontogenetic research to understand the variation underlying the ruminant digestive system.

Additional material

Additional figures are given in the supplementary material. The data used for the statistical evaluations in this study are available as a supplementary spreadsheet file.

References

Akbari H, Moradi HV, Rezaie HR, Baghestani N (2016) Winter foraging of chinkara (*Gazella bennettii shikarii*) in central Iran. Mammalia 80:163-169

Archer D, Sanson G (2002) Form and function of the selenodont molar in southern African ruminants in relation to their feeding habits. Journal of Zoology (London) 257:13-26

Bailey CB (1986) Growth of digestive organs and their contents in holstein steers: relation to body weight and diet. Canadian Journal of Animal Science 66:653-661

Becker RB, Dix Arnold PT, Marshall SP, Wino J (1952) Early development and function of the bovine stomach. Journal of Dairy Science 35:504-505

Bonin M, Tremblay JP, Côté SD (2016) Contributions of digestive plasticity to the ability of white-tailed deer to cope with a low-quality diet. Journal of Mammalogy 97:1406-1413

Booyse DG, Dehority BA (2012) Protozoa and digestive tract parameters in Blue wildebeest (*Connochaetes taurinus*) and Black wildebeest (*Connochaetes gnou*), with description of *Entodinium taurinus* n. sp. European Journal of Protistology 48:283-289

Burnham KP, Anderson DR (2001) Kullback-Leibler information as a basis for strong inference in ecological studies. Wildlife Research 28:111-119

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical Information-Theoretic approach. Springer-Verlag, New York

Calder WA (1996) Size, function and life history. Havard University Press, Cambridge, MA

Cantalapiedra JL, FitzJohn RG, Kuhn TS, Fernández MH, DeMiguel D, Azanza B, Morales J, Mooers AØ (2014) Dietary innovations spurred the diversification of ruminants during the Caenozoic. Proceedings of the Royal Society B 281:20132746

Cerling TE, Andanje SA, Blumenthal SA, Brown FH, Chritz KL, Harris JM, Hart JA, Kirera FM, Kaleme P, Leakey LN, Leakey MG (2015) Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma. Proceedings of the National Academy of Science 112:11467-11472

Church EC HW (1978) Ruminoreticular characteristics of elk. Journal of Wildlife Management 42: 654-659

Clauss M, Lechner-Doll M, Streich WJ (2002) Faecal particle size distribution in captive wild ruminants: an approach to the browser/grazer dichotomy from the other end. Oecologia 131:343-349

Clauss M, Hummel J, Vercammen F, Streich WJ (2005) Observations on the macroscopic digestive anatomy of the Himalayan Tahr (*Hemitragus jemlahicus*). Anatomia Histologia Embryologica 34:276-278

Clauss M, Hofmann RR, Hummel J, Adamczewski J, Nygren K, Pitra C, Streich WJ, Reese S (2006a) The macroscopic anatomy of the omasum of free-ranging moose (*Alces alces*) and muskoxen (*Ovibos moschatus*) and a comparison of the omasal laminal surface area in 34 ruminant species. Journal of Zoology 270:346-358

Clauss M, Hummel J, Streich WJ (2006b) The dissociation of the fluid and particle phase in the forestomach as a physiological characteristic of large grazing ruminants: an

evaluation of available, comparable ruminant passage data. European Journal of Wildlife Research 52:88-98
Clauss M, Hummel J, Völlm J, Lorenz A, Hofmann RR (2006c) The allocation of a ruminant feeding type to the okapi (*Okapia johnstoni*) on the basis of morphological parameters. In: Fidgett A, Clauss M, Eulenberger K, Hatt J, M, Hume I, Janssens G, Nijboer J (eds) Zoo animal nutrition III. Filander Verlag, Fürth, Germany, pp 253-270
Clauss M, Hofmann RR, Streich WJ, Fickel J, Hummel J (2008a) Higher masseter mass in grazing than in browsing ruminants. Oecologia 157:377-385
Clauss M, Kaiser T, Hummel J (2008b) The morphophysiological adaptations of browsing and grazing mammals. In: Gordon IJ, Prins HHT (eds) The ecology of browsing and grazing. Springer, Heidelberg, pp 47-88
Clauss M, Fritz J, Bayer D, Hummel J, Streich WJ, Südekum K-H, Hatt J-M (2009a) Physical characteristics of rumen contents in two small ruminants of different feeding type, the mouflon (*Ovis ammon musimon*) and the roe deer (*Capreolus capreolus*). Zoology 112:195-205
Clauss M, Fritz J, Bayer D, Nygren K, Hammer S, Hatt J-M, Südekum K-H, Hummel J (2009b) Physical characteristics of rumen contents in four large ruminants of different feeding type, the addax (*Addax nasomaculatus*), bison (*Bison bison*), red deer (*Cervus elaphus*) and moose (*Alces alces*). Comparative Biochemistry and Physiology A 152:398-406
Clauss M, Hofmann RR, Fickel J, Streich WJ, Hummel J (2009c) The intraruminal papillation gradient in wild ruminants of different feeding types: implications for rumen physiology. Journal of Morphology 270:929-942
Clauss M, Reese S, Eulenberger K (2009d) Macroscopic digestive anatomy of a captive lowland anoa (*Bubalus depressicornis*). In: Clauss M, Fidgett AL, Hatt J-M, Huisman T, Hummel J, Janssen G, Nijboer J, Plowman A (eds) Zoo animal nutrition IV. Filander Verlag, Fürth, pp 257-265
Clauss M, Hofmann RR, Streich WJ, Fickel J, Hummel J (2010a) Convergence in the macroscopic anatomy of the reticulum in wild ruminant species of different feeding types and a new resulting hypothesis on reticular function. Journal of Zoology 281:26-38
Clauss M, Hume ID, Hummel J (2010b) Evolutionary adaptations of ruminants and their potential relevance for modern production systems. Animal 4:979-992
Clauss M, Müller K, Fickel J, Streich WJ, Hatt J-M, Südekum K-H (2011) Macroecology of the host determines microecology of endobionts: protozoal faunas vary with wild ruminant feeding type and body mass. Journal of Zoology 283:169–185
Clauss M, Hofmann RR (2014) The digestive system of ruminants, and peculiarities of (wild) cattle. In: Melletti M, Burton J (eds) Ecology, evolution and behaviour of wild cattle: implications for conservation. Cambridge University Press, Cambridge UK, pp 57-62
Clauss M, Rössner GE (2014) Old world ruminant morphophysiology, life history, and fossil record: exploring key innovations of a diversification sequence. Annales Zoologici Fennici 51:80-94
Clauss M, Steuer P, Erlinghagen-Lückerath K, Kaandorp J, Fritz J, Südekum K-H, Hummel J (2015) Faecal particle size: digestive physiology meets herbivore diversity. Comparative Biochemistry and Physiology A 179:182-191
Clauss M, Hummel J (2017) Physiological adaptations of ruminants and their potential relevance for production systems. Revista Brasileira de Zootecnia 46:606-613
Codron D, Brink JS, Rossouw L, Clauss M (2008) The evolution of ecological specialization in southern African ungulates: competition- or physical environmental turnover? Oikos 117:344-353

Codron D, Clauss M (2010) Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species. Canadian Journal of Zoology 88:1129-1138
DeMiguel D, Fortelius M, Azanza B, Morales J (2008) Ancestral feeding state of ruminants reconsidered: earliest grazing adaptation claims a mixed condition for Cervidae. BMC Evolutionary Biology 8:13
Demment MW, Longhurst WH (1987) Browsers and grazers: constraints on feeding ecology imposed by gut morphology and body size. In: Santana OP, da Silva AG, Foote WC (eds) Proceedings of the IVth International Conference on Goats. Departimento de Disuao de Tecnologia, Brasilia, Brasilien, pp 989-1004
Dittmann MT, Hummel J, Hammer S, Arif A, Hebel C, Müller DWH, Fritz J, Steuer P, Schwarm A, Kreuzer M, Clauss M (2015a) Digesta retention in gazelles in comparison to other ruminants: Evidence for taxon-specific rumen fluid throughput to adjust digesta washing to the natural diet. Comparative Biochemistry and Physiology A 185:58-68
Dittmann MT, Runge U, Ortmann S, Lang RA, Moser D, Galeffi C, Schwarm A, Kreuzer M, Clauss M (2015b) Digesta retention patterns of solutes and different-sized particles in camelids compared with ruminants and other foregut fermenters. Journal of Comparative Physiology B 185:559-573
Fonseca CC, Machado GV, Espeschit CJB, das Neves MTD, do Anjos Benjamin L, Vasconcellos RS (1998) Dados macroscópicos sobre as lâminas do omaso de caprinos mestiços. Arquivos de Ciências Veterinárias e Zoologia da UNIPAR 1:41-45
Fritz J, Hummel J, Kienzle E, Arnold C, Nunn C, Clauss M (2009a) Comparative chewing efficiency in mammalian herbivores. Oikos 118:1623-1632
Fritz SA, Bininda-Emonds ORP, Purvis A (2009b) Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. Ecology Letters 12:538-549
Gagnon M, Chew AE (2000) Dietary preferences in extant African Bovidae. Journal of Mammalogy 81:490-511
Garcia A, Masot J, Franco A, Gazquez A, Redondo E (2013) Histomorphometric and immunohistochemical study of the goat omasum during prenatal development. Histology and Histopathology 28:737-748
Garrod AH (1877) Notes on the visceral anatomy and osteology of the ruminants, with a suggestion regarding a method of expressing the relations of species by means of formulae. Proceedings of the Zoological Society of London:2-18
Geiger G, Hofmann RR, König R (1977) Vergleichend-anatomische Untersuchungen an den Vormägen von Damwild (*Cervus dama*) und Muffelwild (*Ovis ammon musimon*). Säugetierkundliche Mitteilungen 25:7-21
Gordon IJ, Illius AW (1988) Incisor arcade structure and diet selection in ruminants. Functional Ecology 2:15-22
Hamada T (1973) Feed utilization and anatomical adaptation of kids after removal of compartments of forestomach or omasal laminae. Journal of Dairy Science 56:473-483
Heywood JJN (2010) Functional anatomy of bovid upper molar occlusal surfaces with respect to diet. Journal of Zoology 281:1-11
Hofmann RR (1969) Zur Topographie und Morphologie des Wiederkäuermagens im Hinblick auf seine Funktion (nach vergleichenden Untersuchungen an Material ostafrikanischer Wildarten). Zentralblatt für Veterinärmedizin Supplement 10:1-180
Hofmann RR (1973) The ruminant stomach. East African Literature Bureau, Nairobi

Hofmann RR, Geiger G, König R (1976) Vergleichend-anatomische Untersuchungen an der Vormagenschleimhaut von Rehwild (*Capreolus capreolus*) und Rotwild (*Cervus elaphus*). Zeitschrift für Säugetierkunde 41:167-193

Hofmann RR (1988) Morphophysiological evolutionary adaptations of the ruminant digestive system. In: Dobson A, Dobson MJ (eds) Aspects of digestive physiology in ruminants. Cornell University Press, Ithaca, NY, pp 1-20

Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:443-457

Hofmann RR, Knight MH, Skinner JD (1995) On structural characteristics and morphophysiological adaptation of the springbok (*Antidorcas marsupialis*) digestive system. Transactions of the Royal Society of South Africa 50:125-142

Hofmann RR, Streich WJ, Fickel J, Hummel J, Clauss M (2008) Convergent evolution in feeding types: salivary gland mass differences in wild ruminant species. Journal of Morphology 269:240-257

Holand Ø, Staaland H (1995) Mineral absorption and secretion patterns in the alimentary tract of the roe deer (*Capreolus capreolus*). Comparative Biochemistry and Physiology A 110:243-252

Holtenius K, Björnhag G (1989) The significance of water absorption and fibre digestion in the omasum of sheep, goats and cattle. Comparative Biochemistry and Physiology A 94:105-109

Hummel J, Steuer P, Südekum K-H, Hammer S, Hammer C, Streich WJ, Clauss M (2008) Fluid and particle retention in the digestive tract of the addax antelope (*Addax nasomaculatus*) – adaptations of a grazing desert ruminant. Comparative Biochemistry and Physiology A 149:142-149

Hummel J, Hammer S, Hammer C, Ruf J, Lechenne M, Clauss M (2015) Solute and particle retention in a small grazing antelope, the blackbuck (*Antilope cervicapra*). Comparative Biochemistry and Physiology A 182:22-26

Jerbi H, Pérez W (2013) Gross anatomy of the stomach of *Cervus elaphus barbarus*. International Journal of Morphology 31:388-391

Jerbi H, Bayoudh M, Clauss M, Pérez W (2016) Gross anatomy of the stomach of the dorcas gazelle (*Gazella dorcas*). International Journal of Morphology 34:1266-1270

Jiang Z, Hamasaki S, Ueda H, Kitahara M, Takatsuki S, Kishimoto M (2006) Sexual variations in food quality and gastrointestinal features of sika deer (*Cervus nippon*) in Japan during winter: implications for feeding strategy. Zoological Science 23:543-549

Kaiser TM, Fickel J, Streich WJ, Hummel J, Clauss M (2010) Enamel ridge alignment in upper molars of ruminants in relation to their natural diet. Journal of Zoology 281:12-25

Langer P (1973) Vergleichend-anatomische Untersuchungen am Magen der Artiodactyla. Gegenbaurs Morphologisches Jahrbuch 119:514-561, 633-695

Langer P (1988) The mammalian herbivore stomach. Gustav Fischer Verlag, Stuttgart/New York

Lauwers H (1973) Morfologische bijdrage tot de kennis von her resorberend vermogen van rundercoormagen. Mededelingen van de Faculteit Diergeneeskunde Rijksuniversiteit Gent 17:1-261

Lechner I, Barboza P, Collins W, Fritz J, Günther D, Hattendorf B, Hummel J, Südekum K-H, Clauss M (2010) Differential passage of fluids and different-sized particles in fistulated oxen (*Bos primigenius* f. *taurus*), muskoxen (*Ovibos moschatus*), reindeer (*Rangifer tarandus*) and moose (*Alces alces*): rumen particle size discrimination is independent from contents stratification. Comparative Biochemistry and Physiology A 155:211-222

Lechner-Doll M, Kaske M, von Engelhardt W (1991) Factors affecting the mean retention time of particles in the forestomach of ruminants and camelids. In: Tsuda T, Sasaki Y, Kawashima R (eds) Physiological aspects of digestion and metabolism in ruminants. Academic Press, San Diego CA, pp 455-482

Ledger H, Smith N (1964) The carcass and body composition of Uganda kob. Journal of Wildlife Management 28:827-829

Lentle RG, Stafford KJ, Henderson IM (1998) Omasal anatomy in New Zealand red and fallow deer: an exploratory multivariate analysis. Anatomia Histologia Embryologia 27:83-87

Li J, Yuan L, Zhou H (2000) Anatomical and morphological features of the stomach of Mongolian gazelle. Journal of Northeast Forestry University 28:67-71

Mathiesen SD, Vader MA, Raedergard VB, Sormo W, Haga OE, Tyler NJC, Hofmann RR (2000) Functional anatomy of the omasum in high arctic Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and Norwegian reindeer (*Rangifer tarandus tarandus*). Acta Veterinaria Scandinavica 41:25-40

McSweeney C (1988) A comparative study of the anatomy of the omasum in domesticated ruminants. Australian Veterinary Journal 65:205-207

Meier AR, Schmuck U, Meloro C, Clauss M, Hofmann RR (2016) Convergence of macroscopic tongue anatomy in ruminants and scaling relationships with body mass or tongue length. Journal of Morphology 277:351-362

Müller DWH, Bingaman Lackey L, Streich WJ, Fickel J, Hatt J-M, Clauss M (2011a) Mating system, feeding type and ex-situ conservation effort determine life expectancy in captive ruminants. Proceedings of the Royal Society B 278:2076-2080

Müller DWH, Caton J, Codron D, Schwarm A, Lentle R, Streich WJ, Hummel J, Clauss M (2011b) Phylogenetic constraints on digesta separation: variation in fluid throughput in the digestive tract in mammalian herbivores. Comparative Biochemistry and Physiology A 160:207-220

Nagy JG, Regelin WL (1975) Comparison of digestive organ size of three deer species. Journal of Wildlife Management 39:621-624

Orme D, Freckleton RP, Thomas G, Petzoldt T, Fritz SA, Isaac NJB, Pearse W (2013) caper: Comparative Analyses of Phylogenetics and Evolution in R. R package version 0.5.2. https://CRAN.R-project.org/package=caper.

Osman AH, Berg R (1982) Studies on the histogenesis of the Tunica mucosa of the stomach of the Egyptian water buffalo (*Bos bubalus*). IV. Histogenesis of the omasal mucosa. Anatomischer Anzeiger 151:467-471

Pérez W, Ungerfeld R (2012) Gross anatomy of the stomach of the pampas deer (*Ozotoceros bezoarticus*). Zoologia 29:337-342

Pérez W, Vazquez N (2012) Gross anatomy of the gastrointestinal tract in the Brown Brocket deer (*Mazama gouazoubira*). Journal of Morphological Science 29:148-150

Pérez W, Erdogan S, Ungerfeld R (2015) Anatomical study of the gastrointestinal tract in free‐living Axis deer (*Axis axis*). Anatomia Histologia Embryologia 44:43-49

Pérez W, König HE, Jerbi H, Clauss M (2016) Macroanatomical aspects of the gastrointestinal tract of the alpaca (*Vicugna pacos*) and dromedary (*Camelus dromedarius*). Vertebrate Zoology 66:419-425

Pfeiffer C (1993) Vergleichend-morphologische Untersuchungem am Verdauungstrakt des chinesischen Muntjak (*Muntiacus reevesii*) einschliesslich saisonaler Veränderungen an der Vormagenschleimhaut, Dissertation, Giessen, Germany

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2011) nlme: linear and nonlinear mixed effects models. R package version 3 1–102 Available at https://cranr-projectorg/web/packages/nlme/

R_Core_Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/
Rduch V (2016) Diet of the puku antelope (*Kobus vardonii*) and dietary overlap with selected other bovids in Kasanka National Park, Zambia. Mammal Research 61:289-297
Redondo E, Masot J, García A, Franco A (2011) Ontogenesis of the omasum: A comparative analysis of the Merino sheep and Iberian red deer. Histology and Histopathology 26:1135-1144
Reissig L (1995) Der südafrikanische Spiessbock (Oryx gazella gazella), vergleichend anatomische Untersuchungen einschliesslich saisonaler Veränderungen der VormagenschleimhautFreie Universität Berlin, Berlin
Sauer C, Bertelsen MF, Hammer S, Lund P, Weisbjerg MR, Clauss M (2016a) Macroscopic digestive tract anatomy of two small antelopes, the blackbuck (*Antilope cervicapra*) and the Arabian sand gazelle (*Gazella subgutturosa marica*). Anatomia Histologia Embryologia 45:392-398
Sauer C, Bertelsen MF, Lund P, Weisbjerg MR, Clauss M (2016b) Quantitative macroscopic anatomy of the giraffe (*Giraffa camelopardalis*) digestive tract. Anatomia Histologia Embryologia 45:338-349
Sauer C, Hammer C, Bertelsen MF, Tütken T, Clauss M, Hammer S (2017) Quantitative macroscopic digestive tract anatomy of the beira (*Dorcatragus megalotis*). Journal of Zoo and Aquarium Research 4:174-179
Serbent MP, Periago ME, Leynaud GC (2011) *Mazama gouazoubira* (Cervidae) diet during the dry season in the arid Chaco of Córdoba (Argentina). Journal of Arid Environments 75:87-90
Sibbald AM, Milne JA (1993) Physical characteristics of the alimentary tract in relation to seasonal changes in voluntary food intake by the red deer (*Cervus elaphus*). Journal of Agricultural Science 120:99-102
Snelling EP, Maloney SK, Farrell AP, Meyer LC, Izwan A, Fuller A, Mitchell D, Haw A, Costello MA, Seymour RS (2018) Scaling of morphology and ultrastructure of hearts among wild African antelope. Journal of Experimental Biology 221:jeb184713
Staaland H, Adamczewski JZ, Gunn A (1997) A comparison of digestive tract morphology in muskoxen and caribou from Victoria Island, Northwest Territories, Canada. Rangifer 17:17-19
Stafford KJ, Stafford YM (1993) The anatomy of the omasum of some Zambian game species. Anatomia Histologia Embryologia 22:342-347
Stillwell RC, Shingleton AW, Dworkin I, Frankino WA (2016) Tipping the scales: evolution of the allometric slope independent of average trait size. Evolution 70:433-444
Sutherland TM (1988) Particle separation in the forestomach of sheep. In: Dobson A, Dobson MJ (eds) Aspects of digestive physiology in ruminants. Cornell University Press, Ithaca, NY, pp 43-73
Tahas SA, Martin Jurado O, Hammer S, Arif A, Reese S, Hatt J-M, Clauss M (2017) Gross measurements of the digestive tract and visceral organs of addax antelope (*Addax nasomaculatus*) following a concentrate or forage feeding regime. Anatomia Histologia Embryologia 46:282-293
Takatsuki S (1988) The weight contributions of stomach compartments of sika deer. Journal of Wildlife Management 52:313-316
Tiwari GP, Jamdar MN (1970) Studies on the gross and histological structure and development of the fore-stomachs of Indian water-buffalo-calf in early postnatal life with reference to normal feeding. III. Omasum. Indian Journal of Animal Sciences 40:574-578

Trautmann A, Schmitt I (1935) Experimentelle Untersuchungen zur Frage der Psalterfunktion. Deutsche Tierärztliche Wochenschrift 12:177-179
Vermeij GJ (2013) On escalation. Annual Review of Earth and Planetary Sciences 41:1-19
Wardrop ID (1961) Some preliminary observations on the histological development of the fore-stomachs of the lamb I. Histological changes due to age in the period from 46 days of foetal life to 77 days of post-natal life. Journal of Agricultural Science Cambridge 57:335-341
Werner A (1990) Vergleichende morphometrische Untersuchungen am Blättermagen von 17 Wiederkäuern unterschiedlicher Ernährungstypen, Dissertation Justus-Liebig-Universität, Giessen
Yamamoto Y, Kitamura N, Yamada J, Andren A, Yamashita T (1994) Morphological study of the surface structure of the omasal laminae in cattle, sheep and goats. Anatomia, Histologia, Embryologia 23:166-176
Zerbe P, Clauss M, Codron D, Bingaman Lackey L, Rensch E, Streich WJ, Hatt J-M, Müller DWH (2012) Reproductive seasonality in captive wild ruminants: implications for biogeographical adaptation, photoperiodic control, and life history. Biological Reviews 87:965-990

Table 1 Results of statistical analyses using generalized least squares (GLS) or phylogenetic generalized least squares (PGLS, accounting for phylogeny) with (log-transformed) omasum measures as the dependent variable, body mass (BM) as the independent variable (Type I model), and the proportion of grass in the natural diet as covariable that either influenced the intercept (BM+Grass, Type II model) or the allometric exponent (BM*Grass, Type III model). Model fit assessed by Akaike's criterion (ΔAIC)

Measure	**GLS**						**PGLS**						
	Model	**ΔAIC**	**Body mass exponent**	***P***	**Factor/ Interaction**	***P***	**Model**	**ΔAIC**	**λ**	**Body mass exponent**	***P***	**Factor/ Interaction**	***P***
Curvature	**BM*Grass**	**0.00**	0.39 (0.32;0.46)	<0.001	**0.28 (0.131;0.43)**	**<0.001**	**BM*Grass**	**0.00**	0.44	0.37 (0.30;0.44)	<0.001	**0.21 (0.06;0.36)**	**0.007**
(n=84)	BM	10.97	0.49 (0.44;0.54)	<0.001	-	-	BM	4.45	0.54	0.45 (0.39;0.50)	<0.001	-	-
	BM+Grass	11.02	0.48 (0.43;0.53)	<0.001	0.06 (-0.02;0.15)	0.150	BM+Grass	5.15	0.52	0.43 (0.38;0.49)	<0.001	0.05 (-0.03;0.14)	0.233
Length	**BM*Grass**	**0.00**	0.38 (0.32;0.43)	<0.001	**0.19 (0.06;0.31)**	**0.004**	**BM*Grass**	**0.00**	0.31	0.36 (0.30;0.42)	<0.001	**0.15 (0.02;0.27)**	**0.026**
(n=81)	BM	4.59	0.44 (0.40;0.47)	<0.001	-	-	**BM**	**1.57**	0.37	0.41 (0.37;0.45)	<0.001	-	-
	BM+Grass	6.57	0.43 (0.39;0.47)	<0.001	0.02 (-0.05;0.09)	0.634	BM+Grass	2.87	0.36	0.40 (0.35;0.45)	<0.001	0.03 (-0.04;0.11)	0.364
Height	**BM**	**0.00**	0.44 (0.40;0.50)	<0.001	-	-	**BM**	**0.00**	0.42	0.40 (0.34;0.46)	<0.001	-	-
(n=81)	**BM*Grass**	**0.19**	0.39 (0.32;0.46)	<0.001	***0.15 (-0.02;0.32)***	***0.093***	**BM+Grass**	**1.43**	0.39*	0.39 (0.33;0.46)	<0.001	0.05 (-0.06;0.15)	0.396
	BM+Grass	**0.90**	0.43 (0.38;0.49)	<0.001	0.05 (-0.04;0.14)	0.262	BM*Grass	2.03	0.32*	0.36 (0.28;0.44)	<0.001	0.12 (-0.06;0.30)	0.206
1st order leaves	**BM*Grass**	**0.00**	0.07 (0.02;0.12)	0.010	***0.11 (0.00;0.22)***	***0.052***	**BM*Grass**	**0.00**	0.29*	0.07 (0.02;0.13)	0.013	**0.13 (0.01;0.25)**	**0.035**
(n=68)	**BM+Grass**	**1.73**	0.10 (0.07;0.14)	<0.001	**0.08 (0.03;0.14)**	**0.006**	BM+Grass	2.43	0.00*	0.10 (0.07;0.14)	<0.001	**0.08 (0.03;0.14)**	**0.006**
	BM	7.34	0.12 (0.08;0.16)	<0.001	-	-	BM	3.86	0.51	0.13 (0.09;0.17)	<0.001	-	-
2nd order leaves	**BM+Grass**	**0.00**	0.14 (0.07;0.21)	<0.001	0.10 (-0.02;0.22)	0.113	**BM+Grass**	**0.00**	0.35	0.11 (0.03;0.18)	0.010	**0.13 (0.01;0.26)**	**0.041**
(n=62)	**BM**	**0.38**	0.15 (0.09;0.22)	<0.001			**BM*Grass**	**1.91**	0.35	0.08 (-0.03;0.19)	0.147	0.07 (-0.16;0.30)	0.555
	BM*Grass	**1.83**	0.11 (0.01;0.21)	0.039	0.08 (-0.15;0.31)	0.479	BM	2.20	0.33	0.13 (0.06;0.21)	<0.001	-	-
Total leaves	**BM+Grass**	**0.00**	0.41 (0.31;0.51)	<0.001	**0.20 (0.01;0.39)**	**0.041**	**BM+Grass**	**0.00**	0.72***	0.35 (0.23;0.47)	<0.001	***0.21 (-0.00;0.41)***	***0.059***
(n=47)	**BM*Grass**	**0.40**	0.34 (0.20;0.48)	<0.001	0.24 (-0.09;0.57)	0.167	**BM*Grass**	**0.64**	0.65***	0.28 (0.12;0.44)	0.002	0.24 (-0.12;0.60)	0.205
	BM	2.13	0.45 (0.35;0.55)	<0.001			**BM**	**0.86**	0.91*	0.37 (0.25;0.49)	<0.001	-	-
Surface	**BM*Grass**	**0.00**	0.99 (0.71;1.26)	<0.001	**0.71 (0.14;1.27)**	**0.019**	**BM*Grass**	**0.00**	0.24*	1.00 (0.73;1.28)	<0.001	**0.72 (0.15;1.28)**	**0.018**
(n=37)	BM+Grass	3.56	1.26 (1.08;1.43)	<0.001	**0.37 (0.07;0.67)**	**0.021**	BM+Grass	3.81	0.26*	1.26 (1.06;1.46)	<0.001	**0.37 (0.05;0.70)**	**0.030**
	BM	6.89	1.30 (1.11;1.48)	<0.001	-	-	BM	6.20	0.48*	1.33 (1.11;1.54)	<0.001	-	-
Organ tissue	**BM*Grass**	**0.00**	0.98 (0.79;1.18)	<0.001	**0.75 (0.27;1.22)**	**0.004**	**BM*Grass**	**0.00**	0.90	0.91 (0.71;1.10)	<0.001	**0.61 (0.19;1.03)**	**0.007**
(n=43)	BM	4.79	1.22 (1.07;1.36)	<0.001	-	-	BM	3.77	0.89	1.11 (0.96;1.26)	<0.001	-	-
	BM+Grass	6.85	1.21 (1.06;1.35)	<0.001	0.08 (-0.19;0.35)	0.561	BM+Grass	5.83	0.90	1.10 (0.94;1.26)	<0.001	0.07 (-0.20;0.34)	0.629
Contents	**BM**	**0.00**	1.24 (1.04;1.45)	<0.001	-	-	**BM**	**0.00**	0.57	1.21 (0.98;1.43)	<0.001	-	-
(n=30)	BM+Grass	2.16	1.23 (1.02;1.44)	<0.001	0.14 (-0.27;0.56)	0.499	BM+Grass	2.48	0.57	1.21 (0.97;1.44)	<0.001	-0.01 (-0.43;0.41)	0.971
	BM*Grass	3.01	1.09 (0.80;1.38)	<0.001	0.53 (-0.24;1.30)	0.187	BM*Grass	4.11	0.51*	1.11 (0.82;1.41)	<0.001	0.38 (-0.38;1.14)	0.333

Best models (dAIC<2) set in bold; significant factors/interaction set in bold (with 0.05<P<0.01 set in italics); body mass exponents whose confidence interval include geometric scaling set in grey shading
λ significantly different from 0 and 1 unless indicated: *significantly different from 1 but not from 0; **significantly different from 0 but not from 1; ***not significantly different from 0 or 1

Table 2 Results of statistical analyses using generalized least squares (GLS) or phylogenetic generalized least squares (PGLS, accounting for phylogeny) with (log-transformed) omasum measures as the dependent variable, body mass (BM) as the independent variable (Type I model), and the proportion of grass in the natural diet or the intrauminal papillation gradient (rSEF) as covariable that either influenced the intercept (BM+Grass/rSEF, Type II model) or the allometric exponent (BM*Grass/rSEF, Type III model). Model fit assessed by Akaike's criterion (ΔAIC)

Measure	GLS						PGLS						
	Model	ΔAIC	Body mass exponent	*P*	Factor/ Interaction	*P*	Model	ΔAIC	λ	Body mass exponent	*P*	Factor/ Interaction	*P*
Curvature	**BM*Grass**	**0.00**	0.37 (0.30;0.44)	<0.001	**0.21 (0.06;0.37)**	**0.011**	**BM*Grass**	**0.00**	0.89***	0.34 (0.26;0.42)	<0.001	**0.20 (0.04;0.37)**	**0.021**
(n=46)	BM+Grass	4.60	0.43 (0.38;0.49)	<0.001	**0.14 (0.05;0.23)**	**0.003**	BM+Grass	3.08	0.99**	0.41 (0.35;0.47)	<0.001	**0.12 (0.03;0.22)**	**0.012**
	BM*rSEF	7.65	0.29 (0.13;0.45)	0.001	***0.22 (-0.01;0.45)***	***0.064***	BM+rSEF	4.36	1.00**	0.41 (0.34;0.47)	<0.001	**0.21 (0.03;0.38)**	**0.024**
	BM+rSEF	8.91	0.43 (0.38;0.49)	<0.001	**0.18 (0.02;0.33)**	**0.031**	BM*rSEF	4.41	1.00**	0.30 (0.13;0.46)	0.001	0.18 (-0.06;0.41)	0.145
	BM	11.53	0.46 (0.40;0.52)	<0.001	-	-	BM	7.55	1.00**	0.44 (0.37;0.50)	<0.001	-	-
Length	**BM*rSEF**	**0.00**	0.23 (0.11;0.34)	<0.001	**0.23 (0.07;0.39)**	**0.007**	**BM*rSEF**	**0.00**	0.67***	0.24 (0.12;0.36)	<0.001	**0.18 (0.01;0.34)**	**0.040**
(n=45)	BM*Grass	4.71	0.34 (0.28;0.39)	<0.001	**0.16 (0.04;0.29)**	**0.015**	**BM+rSEF**	**1.33**	0.95**	0.35 (0.30;0.40)	<0.001	**0.20 (0.07;0.33)**	**0.003**
	BM+rSEF	5.48	0.38 (0.34;0.42)	<0.001	**0.18 (0.06;0.29)**	**0.004**	BM*Grass	4.29	0.57***	0.32 (0.26;0.38)	<0.001	**0.15 (0.01;0.28)**	**0.037**
	BM+Grass	8.72	0.39 (0.35;0.43)	<0.001	**0.09 (0.02;0.16)**	**0.021**	BM+Grass	6.03	0.86**	0.36 (0.31;0.41)	<0.001	**0.08 (0.08;0.16)**	**0.036**
	BM	12.08	0.41 (0.36;0.45)	<0.001			BM	8.29	0.96**	0.38 (0.33;0.43)	<0.001	-	-
Height	**BM*Grass**	**0.00**	0.38 (0.31;0.46)	<0.001	***0.16 (-0.00;0.33)***	***0.058***	**BM*Grass**	**0.00**	0.00*	0.38 (0.31;0.46)	<0.001	***0.16 (-0.00;0.32)***	***0.058***
(n=45)	**BM+Grass**	**1.45**	0.43 (0.38;0.49)	<0.001	**0.10 (0.01;0.18)**	**0.039**	**BM+Grass**	**1.57**	0.00*	0.43 (0.38;0.49)	<0.001	**0.10 (0.01;0.18)**	**0.039**
	BM+rSEF	2.26	0.43 (0.38;0.49)	<0.001	***0.15 (-0.00;0.30)***	***0.061***	BM+rSEF	2.38	0.00*	0.43 (0.38;0.49)	<0.001	***0.15 (-0.00;0.30)***	***0.061***
	BM	3.66	0.45 (0.40;0.51)	<0.001	-	-	BM	3.89	0.00*	0.45 (0.40;0.51)	<0.001	-	-
	BM*rSEF	4.34	0.38 (0.22;0.54)	<0.001	0.07 (-0.15;0.30)	0.523	BM*rSEF	4.34	0.00*	0.38 (0.22;0.54)	<0.001	0.07 (-0.15;0.30)	0.523
1st order leaves	**BM*Grass**	**0.00**	0.10 (0.04;0.15)	0.001	***0.12 (-0.01;0.24)***	***0.069***	**BM*Grass**	**0.00**	0.00*	0.10 (0.04;0.15)	0.001	***0.12 (-0.01;0.24)***	***0.069***
(n=43)	**BM+Grass**	**1.13**	0.13 (0.09;0.17)	<0.001	**0.11 (0.05;0.17)**	**0.002**	**BM+Grass**	**1.26**	0.00*	0.13 (0.09;0.17)	<0.001	**0.11 (0.05;0.17)**	**0.002**
	BM+rSEF	7.65	0.13 (0.09;0.18)	<0.001	***0.12 (0.00;0.23)***	***0.053***	BM+rSEF	7.68	0.08*	0.14 (0.10;0.18)	<0.001	***0.11 (-0.01;0.23)***	***0.072***
	BM	9.28	0.15 (0.12;0.19)	<0.001	-	-	BM	8.51	0.22*	0.16 (0.11;0.20)	<0.001	-	-
	BM*rSEF	9.89	0.10 (-0.02;0.22)	0.114	0.05 (-0.13;0.23)	0.588	BM*rSEF	9.62	0.14*	0.10 (-0.02;0.22)	0.121	0.06 (-0.11;0.24)	0.479
2nd order leaves	**BM+Grass**	**0.00**	0.16 (0.08;0.23)	<0.001	**0.13 (0.00;0.25)**	**0.049**	**BM+Grass**	**0.00**	0.00*	0.16 (0.08;0.23)	<0.001	**0.13 (0.00;0.25)**	**0.049**
(n=40)	**BM**	**1.76**	0.18 (0.10;0.26)	<0.001	-	-	**BM**	**1.89**	0.00*	0.18 (0.10;0.26)	<0.001	-	-
	BM*Grass	2.07	0.14 (0.03;0.24)	0.017	0.09 (-0.16;0.33)	0.485	**BM*Grass**	**1.93**	0.00*	0.14 (0.03;0.24)	0.017	0.09 (-0.16;0.33)	0.485
	BM+rSEF	4.13	0.17 (0.09;0.26)	<0.001	0.03 (-0.19;0.25)	0.762	BM+rSEF	4.13	0.00*	0.17 (0.09;0.26)	<0.001	0.03 (-0.19;0.25)	0.763
	BM*rSEF	4.54	0.02 (-0.20;0.25)	0.850	0.23 (-0.09;0.55)	0.160	BM*rSEF	4.38	0.00*	0.02 (-0.20;0.25)	0.851	0.23 (-0.09;0.55)	0.160
Total leaves	**BM+Grass**	**0.00**	0.36 (0.22;0.50)	<0.001	**0.48 (0.16;0.80)**	**0.009**	**BM+Grass**	**0.00**	0.30***	0.34 (0.20;0.49)	<0.001	**0.48 (0.16;0.81)**	**0.009**
(n=23)	BM*Grass	3.03	0.33 (0.16;0.51)	0.001	0.14 (-0.43;0.71)	0.635	BM*Grass	2.12	0.65***	0.29 (0.11;0.47)	0.005	0.27 (-0.28;0.82)	0.349
	BM+rSEF	3.42	0.40 (0.26;0.54)	<0.001	**0.42 (0.03;0.81)**	**0.045**	BM*rSEF	2.30	1.00***	0.12 (-0.23;0.46)	0.515	0.46 (-0.08;1.00)	0.114
	BM*rSEF	4.89	0.19 (-0.18;0.55)	0.328	0.38 (-0.21;0.97)	0.224	BM+rSEF	2.43	0.95***	0.38 (0.23;0.52)	<0.001	**0.44 (0.04;0.84)**	**0.046**
	BM	5.19	0.44 (0.29;0.59)	<0.001	-	-	BM	4.40	1.00***	0.42 (0.27;0.58)	<0.001	-	-
Surface	**BM+Grass**	**0.00**	1.18 (0.94;1.42)	<0.001	**0.64 (0.22;1.07)**	**0.008**	**BM*Grass**	**0.00**	1.00***	0.89 (0.57;1.21)	<0.001	***0.78 (0.02;1.53)***	***0.060***
(n=20)	**BM*Grass**	**0.08**	0.93 (0.58;1.29)	<0.001	***0.68 (-0.08;1.44)***	***0.098***	**BM+Grass**	**1.40**	1.00***	1.12 (0.86;1.37)	<0.001	**0.65 (0.19;1.11)**	**0.014**
	BM*rSEF	3.43	0.56 (-0.10;1.22)	0.114	**1.00 (0.09;1.92)**	**0.047**	BM*rSEF	3.69	1.00***	0.53 (-0.09;1.16)	0.111	**1.03 (0.12;1.93)**	**0.041**
	BM+rSEF	4.89	1.23 (0.97;1.50)	<0.001	***0.55 (-0.04;1.15)***	***0.087***	BM+rSEF	5.90	1.00***	1.18 (0.90;1.46)	<0.001	0.54 (-0.12;1.20)	0.127
	BM	5.26	1.25 (0.98;1.53)	<0.001	-	-	BM	5.92	1.00***	1.19 (0.90;1.48)	<0.001	-	-
Organ tissue	**BM+Grass**	**0.00**	1.16 (0.93;1.39)	<0.001	0.38 (-0.05;0.80)	0.100	**BM*Grass**	**0.00**	1.00***	0.95 (0.65;1.25)	<0.001	0.64 (-0.10;1.39)	0.110
(n=19)	**BM**	**0.06**	1.17 (0.93;1.41)	<0.001	-	-	**BM+Grass**	**0.09**	1.00***	1.12 (0.89;1.36)	<0.001	0.35 (-0.07;0.77)	0.125
	BM*Grass	**1.29**	0.98 (0.66;1.31)	<0.001	0.59 (-0.21;1.38)	0.170	**BM**	**0.11**	1.00***	1.16 (0.92;1.40)	<0.001	-	-
	BM+rSEF	2.42	1.16 (0.92;1.41)	<0.001	0.25 (-0.31;0.80)	0.393	BM+rSEF	2.24	1.00***	1.15 (0.90;1.39)	<0.001	0.23 (-0.35;0.81)	0.443
	BM*rSEF	3.18	0.75 (0.19;1.31)	0.018	0.68 (-0.15;1.52)	0.130	BM*rSEF	2.27	1.00***	0.74 (0.21;1.27)	0.015	0.69 (-0.12;1.49)	0.116

Contents	**BM**	**0.00**	1.03 (0.75;1.31)	<0.001	**-**	**-**	**BM+rSEF**	**0.00**	0.00*	1.05 (0.79;1.30)	<0.001	0.41 (-0.05;0.87)	0.108
(n=13)	**BM+rSEF**	**0.80**	1.05 (0.79;1.30)	<0.001	0.41 (-0.05;0.87)	0.108	**BM**	**0.06**	0.00***	1.03 (0.75;1.31)	<0.001	-	-
	BM+Grass	**1.09**	1.04 (0.78;1.29)	<0.001	0.32 (-0.05;0.70)	0.123	**BM+Grass**	**0.29**	0.00*	1.04 (0.78;1.29)	<0.001	0.32 (-0.05;0.70)	0.123
	BM*rSEF	6.11	1.18 (0.54;1.81)	0.006	-0.21 (-1.15;0.74)	0.675	BM*rSEF	4.07	0.00*	1.18 (0.54;1.81)	0.006	-0.21 (-1.15;0.74)	0.675
	BM*Grass	6.49	1.09 (0.67;1.51)	0.001	-0.15 (-0.99;0.70)	0.742	BM*Grass	4.45	0.00*	1.09 (0.67;1.51)	0.001	-0.15 (-0.99;0.70)	0.742

Best models (dAIC<2) set in bold; significant factors/interaction set in bold (with 0.05<P<0.01 set in italics); body mass exponents whose confidence interval include geometric scaling set in grey shading
λ significantly different from 0 and 1 unless indicated: *significantly different from 1 but not from 0; **significantly different from 0 but not from 1; ***not significantly different from 0 or 1

Table 3 Results of statistical analyses using generalized least squares (GLS) or phylogenetic generalized least squares (PGLS, accounting for phylogeny) with (log-transformed) omasum measures as the dependent variable, body mass (BM) as the independent variable (Type I model), and the proportion of grass in the natural diet or the ratio of particle to fluid retention in the reticulorumen (SF RR) as covariable that either influenced the intercept (BM+Grass/SFRR, Type II model) or the allometric exponent (BM*Grass/SFRR, Type III model). Model fit assessed by Akaike's criterion (ΔAIC)

Measure	GLS						PGLS						
	Model	ΔAIC	Body mass exponent	*P*	Factor/ Interaction	*P*	Model	ΔAIC	λ	Body mass exponent	*P*	Factor/ Interaction	*P*
Curvature	**BM*Grass**	**0.00**	0.37 (0.23;0.51)	<0.001	**0.49 (0.12;0.87)**	**0.018**	**BM+SFRR**	**0.00**	0.71	0.45 (0.35;0.55)	<0.001	**0.14 (0.02;0.26)**	**0.030**
(n=25)	**BM+SFRR**	**0.59**	0.48 (0.38;0.58)	<0.001	***0.12 (0.00;0.24)***	***0.057***	BM*SFRR	2.05	0.82**	0.59 (0.30;0.88)	0.001	-0.08 (-0.23;0.08)	0.331
	BM	**1.95**	0.52 (0.43;0.62)	<0.001		-	BM*Grass	2.31	0.57*	0.38 (0.24;0.51)	<0.001	**0.42 (0.06;0.78)**	**0.033**
	BM+Grass	3.69	0.51 (0.41;0.61)	<0.001	0.11 (-0.11;0.33)	0.326	BM	2.68	0.62	0.50 (0.40;0.60)	<0.001	-	-
	BM*SFRR	3.75	0.48 (0.15;0.80)	0.009	-0.00 (-0.18;0.18)	0.996	BM+Grass	5.00	0.59*	0.49 (0.38;0.60)	<0.001	0.06 (-0.18;0.30)	0.608
Length	**BM*Grass**	**0.00**	0.33 (0.21;0.44)	<0.001	**0.40 (0.09;0.71)**	**0.019**	**BM*Grass**	**0.00**	0.14*	0.33 (0.21;0.45)	<0.001	**0.40 (0.09;0.71)**	**0.020**
(n=24)	**BM+SFRR**	**1.07**	0.42 (0.34;0.50)	<0.001	***0.09 (-0.01;0.19)***	***0.084***	**BM+SFRR**	**0.69**	0.29*	0.42 (0.33;0.50)	<0.001	***0.10 (-0.00;0.21)***	***0.070***
	BM	**1.66**	0.46 (0.38;0.53)	<0.001	-	-	**BM**	**1.85**	0.23*	0.45 (0.37;0.54)	<0.001	-	-
	BM+Grass	3.57	0.45 (0.36;0.53)	<0.001	0.09 (-0.09;0.27)	0.356	BM*SFRR	3.32	0.33*	0.48 (0.21;0.75)	0.002	-0.04 (-0.18;0.11)	0.625
	BM*SFRR	4.18	0.46 (0.19;0.74)	0.004	-0.02 (-0.17;0.12)	0.765	BM+Grass	3.77	0.16*	0.44 (0.36;0.53)	<0.001	0.08 (-0.11;0.27)	0.421
Height	**BM+SFRR**	**0.00**	0.36 (0.28;0.45)	<0.001	**0.13 (0.03;0.24)**	**0.022**	**BM+SFRR**	**0.00**	1.00**	0.34 (0.26;0.43)	<0.001	0.08 (-0.01;0.18)	0.106
(n=25)	BM*SFRR	2.32	0.24 (-0.04;0.52)	0.110	0.07 (-0.08;0.22)	0.390	**BM**	**0.43**	1.00**	0.36 (0.28;0.44)	<0.001	-	-
	BM	3.22	0.41 (0.32;0.50)	<0.001	-	-	BM*SFRR	2.83	1.00***	0.31 (0.05;0.57)	0.030	0.012 (-0.11; 0.15)	0.802
	BM+Grass	5.32	0.40 (0.31;0.49)	<0.001	0.09 (-0.11;0.28)	0.406	BM+Grass	2.99	1.00**	0.37 (0.27;0.46)	<0.001	-0.03 (-0.24;0.18)	0.806
	BM*Grass	7.31	0.34 (0.20;0.49)	<0.001	0.20 (-0.18;0.59)	0.316	BM*Grass	5.86	1.00**	0.37 (0.24;0.50)	<0.001	-0.03 (-0.34;0.29)	0.873
1st order leaves	**BM+Grass**	**0.00**	0.09 (0.04;0.15)	0.004	**0.13 (0.01;0.24)**	**0.040**	**BM+Grass**	**0.00**	0.41***	0.07 (0.01;0.13)	0.038	**0.16 (0.03;0.29)**	**0.024**
(n=22)	**BM+SFRR**	**0.44**	0.09 (0.03;0.15)	0.010	***0.07 (0.00;0.14)***	***0.050***	**BM+SFRR**	**0.36**	0.00*	0.09 (0.03;0.15)	0.010	***0.07 (0.00;0.14)***	***0.050***
	BM	**1.97**	0.10 (0.04;0.17)	0.003			BM	2.21	0.00***	0.10 (0.04;0.17)	0.003	-	-
	BM*Grass	3.24	0.08 (-0.03;0.19)	0.193	0.05 (-0.21;0.31)	0.723	BM*Grass	2.84	0.57***	0.04 (-0.07;0.15)	0.447	0.05 (-0.21;0.31)	0.686
	BM*SFRR	3.83	0.08 (-0.14;0.30)	0.475	0.00 (-0.11;0.12)	0.960	BM*SFRR	3.37	0.52***	0.03 (-0.18;0.24)	0.780	0.02 (-0.09;0.13)	0.728
2nd order leaves	**BM**	**0.00**	0.14 (0.08;0.21)	0.001			**BM+Grass**	**0.00**	1.00**	0.10 (0.03;0.17)	0.010	**0.19 (0.04;0.35)**	**0.023**
(n=20)	**BM+SFRR**	**1.39**	0.14 (0.07;0.20)	0.001	0.05 (-0.03;0.14)	0.227	BM	2.27	0.90***	0.12 (0.05;0.19)	0.004	-	-
	BM+Grass	**1.56**	0.14 (0.07;0.21)	0.001	0.08 (-0.05;0.22)	0.249	BM*Grass	3.13	1.00**	0.11 (-0.00;0.22)	0.075	-0.02 (-0.28;0.23)	0.860
	BM*SFRR	4.28	0.02 (-0.29;0.32)	0.913	0.06 (-0.09;0.21)	0.450	BM+SFRR	4.34	0.75***	0.11 (0.04;0.18)	0.009	0.04 (-0.04;0.13)	0.332
	BM*Grass	4.60	0.09 (-0.06;0.24)	0.268	0.12 (-0.23;0.47)	0.502	BM*SFRR	4.73	0.88**	-0.06 (-0.29;0.16)	0.590	0.09 (-0.02;0.20)	0.126
Total leaves	**BM+SFRR**	**0.00**	0.44 (0.25;0.62)	<0.001	**0.28 (0.05;0.50)**	**0.027**	**BM+Grass**	**0.00**	1.00***	0.22 (-0.01;0.44)	0.076	**0.58 (0.10;1.07)**	**0.032**
(n=19)	**BM+Grass**	**1.80**	0.44 (0.25;0.63)	<0.001	***0.29 (0.00;0.72)***	***0.065***	**BM+SFRR**	**0.11**	0.25*	0.40 (0.21;0.59)	0.001	**0.28 (0.05 to 0.51)**	**0.028**
	BM	2.72	0.47 (0.26;0.67)	<0.001	-	-	BM	2.59	0.92***	0.32 (0.08;0.55)	0.018	-	-
	BM*SFRR	3.75	0.41 (-0.29;1.11)	0.270	0.02 (-0.37;0.40)	0.938	BM*Grass	3.10	1.00***	0.26 (-0.08;0.61)	0.156	-0.13 (-0.88;0.61)	0.731
	BM*Grass	5.51	0.41 (0.05;0.77)	0.041	0.09 (-0.77;0.95)	0.840	BM*SFRR	3.32	0.34***	0.32 (-0.36;0.99)	0.375	0.04 (-0.33;0.41)	0.837
Surface	**BM+Grass**	**0.00**	1.18 (0.94;1.43)	<0.001	**0.60 (0.16;1.05)**	**0.017**	**BM+Grass**	**0.00**	1.00**	1.18 (0.92;1.44)	<0.001	**0.54 (0.08;1.00)**	**0.036**
(n=19)	**BM+SFRR**	**1.69**	1.17 (0.91;1.43)	<0.001	**0.31 (0.04;0.57)**	**0.038**	BM	2.56	1.00**	1.28 (1.01;1.55)	<0.001	-	-
	BM*Grass	3.58	1.12 (0.70;1.54)	<0.001	0.23 (-0.95;1.41)	0.710	BM+SFRR	2.87	0.91***	1.26 (1.00;1.52)	<0.001	***0.26 (-0.02;0.53)***	***0.089***
	BM	3.73	1.24 (0.96;1.51)	<0.001	-	-	BM*Grass	3.23	1.00***	1.16 (0.83;1.50)	<0.001	0.06 (-0.80;0.91)	0.895
	BM*SFRR	4.87	0.88 (0.03;1.74)	0.061	0.15 (-0.28;0.58)	0.506	BM*SFRR	4.09	1.00**	0.73 (-0.08;1.55)	0.098	0.30 (-0.11;0.70)	0.178
Organ tissue	**BM+SFRR**	**0.00**	1.11 (0.93;1.29)	<0.001	**0.32 (0.09;0.54)**	**0.013**	**BM+SFRR**	**0.00**	0.38*	1.09 (0.90;1.28)	<0.001	**0.28 (0.05;0.52)**	**0.032**
(n=20)	**BM*SFRR**	**1.43**	0.74 (0.18;1.30)	0.020	0.22 (-0.10;0.53)	0.193	**BM*SFRR**	**0.99**	0.00*	0.74 (0.18;1.30)	0.020	0.22 (-0.10;0.53)	0.193
	BM	4.24	1.19 (0.99;1.39)	<0.001	-	-	**BM**	**1.43**	0.81***	1.13 (0.92;1.34)	<0.001	-	-
	BM*Grass	4.66	0.97 (0.70;1.24)	<0.001	***0.87 (0.01;1.73)***	***0.064***	**BM+Grass**	**1.60**	0.91**	1.06 (0.83;1.28)	<0.001	0.40 (-0.07;0.87)	0.112
	BM+Grass	5.45	1.16 (0.96;1.36)	<0.001	0.30 (-0.15;0.75)	0.204	BM*Grass	3.09	0.78***	0.98 (0.71;1.23)	<0.001	0.54 (-0.27;1.36)	0.209

Contents	**BM**	**0.00**	1.23 (0.96;1.49)	<0.001	-	-	**BM+SFRR**	**0.00**	0.00*	1.14 (0.87;1.41)	<0.001	0.28 (-0.05;0.61)	0.115
(n=17)	**BM+SFRR**	**0.36**	1.14 (0.87;1.41)	<0.001	0.28 (-0.05;0.61)	0.115	**BM**	**0.14**	0.00*	1.23 (0.96;1.49)	<0.001	-	-
	BM+Grass	**1.21**	1.20 (0.94;1.46)	<0.001	0.42 (-0.16;1.01)	0.178	**BM+Grass**	**0.85**	0.00*	1.20 (0.94;1.46)	<0.001	0.42 (-0.16;1.01)	0.178
	BM*SFRR	4.45	1.22 (0.20;2.25)	0.036	-0.05 (-0.65;0.55)	0.875	BM*SFRR	3.45	0.00*	1.22 (0.20;2.25)	0.036	-0.05 (-0.65;0.55)	0.875
	BM*Grass	5.11	1.14 (0.76;1.52)	<0.001	0.26 (-0.96;1.48)	0.686	BM*Grass	4.11	0.00*	1.14 (0.76;1.52)	<0.001	0.26 (-0.96;1.48)	0.685

Best models (dAIC<2) set in bold; significant factors/interaction set in bold (with 0.05<P<0.01 set in italics); body mass exponents whose confidence interval include geometric scaling set in grey shading
λ significantly different from 0 and 1 unless indicated: *significantly different from 1 but not from 0; **significantly different from 0 but not from 1; ***not significantly different from 0 or 1: †set manually (to match λ of the model with interaction term) as the maximum likelihood model could not be resolved

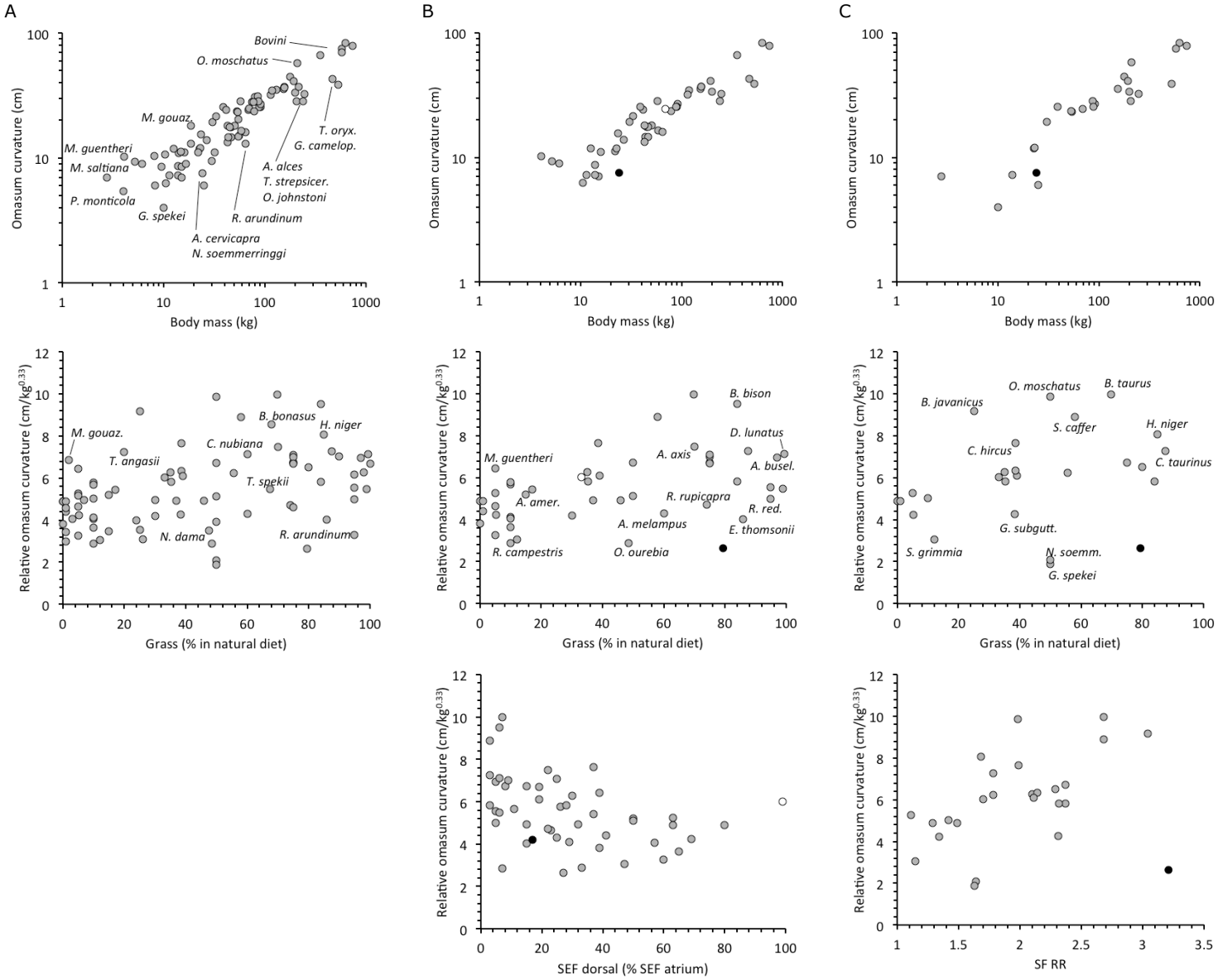

A
B
C
Omasum curvature (cm)
Body mass (kg)
Bovini
O. moschatus
M. gouaz
T. oryx.
G. camelop.
M. guentheri
M. saltiana
A. alces
T. strepsicer.
O. johnstoni
P. monticola
G. spekei
R. arundinum
A. cervicapra
N. soemmerringgi
Relative omasum curvature (cm/kg^0.33)
Grass (% in natural diet)
B. bonasus
H. niger
M. gouaz.
C. nubiana
T. angasii
T. spekii
N. dama
R. arundinum
B. bison
D. lunatus
A. axis
A. busel.
M. guentheri
A. amer.
R. rupicapra
R. red.
A. melampus
E. thomsonii
R. campestris
O. ourebia
B. taurus
O. moschatus
B. javanicus
S. caffer
H. niger
C. hircus
C. taurinus
G. subgutt.
S. grimmia
N. soemm.
G. spekei
SEF dorsal (% SEF atrium)
SF RR

Figure 1 Relationship between the omasum curvature and body mass and the relative omasum curvature and the percentage of grass in the natural diet in ruminant species for (A) the full dataset (cf. Table 1 for statistics); (B) the dataset that comprises species with information on the surface enlargement factor (SEF), including the relationship of the relative omasum curvature and the SEF in the dorsal rumen as percentage of the SEF of the *Atrium ruminis* (a measure for the intraruminal papillation gradient, with larger values indicating a more stratified rumen with potentially higher fluid throughput). Outliers: blackbuck (*Antilope cervicapra* - black dot) and reindeer (*Rangifer tarandus* - white dot, cf. Table 2 for statistics); (C) the dataset that comprises species with information on the selectivity factor in the reticulorumen (SF RR, a measure for the difference between particle and fluid retention in the rumen, with larger values indicating a higher rumen fluid throughput), including the relationship of the relative omasum curvature and the SFRR. Outlier: blackbuck (*Antilope cervicapra* - black dot, cf. Table 3 for statistics).

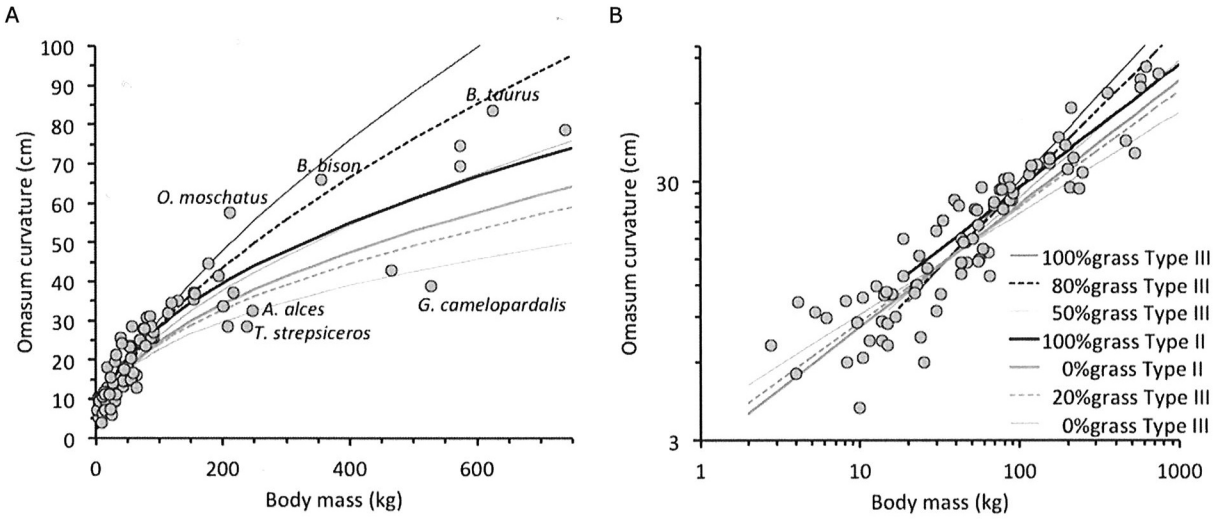


Figure 2 Graphical comparison of a Type II model (allowing only a difference in intercept/allometric factor due to the percentage of grass in the natural diet) and a Type III model (allowing a change in the slope/allometric exponent due to the percentage of grass in the natural diet). Note that while the Type II model does not reflect the data pattern well (and was not significant, cf. Table 1), the range of large species is well represented by the Type III model, whereas the representation of the small species by the model is poor. Variation in the 2-20 kg body size range is not explained well by the model.

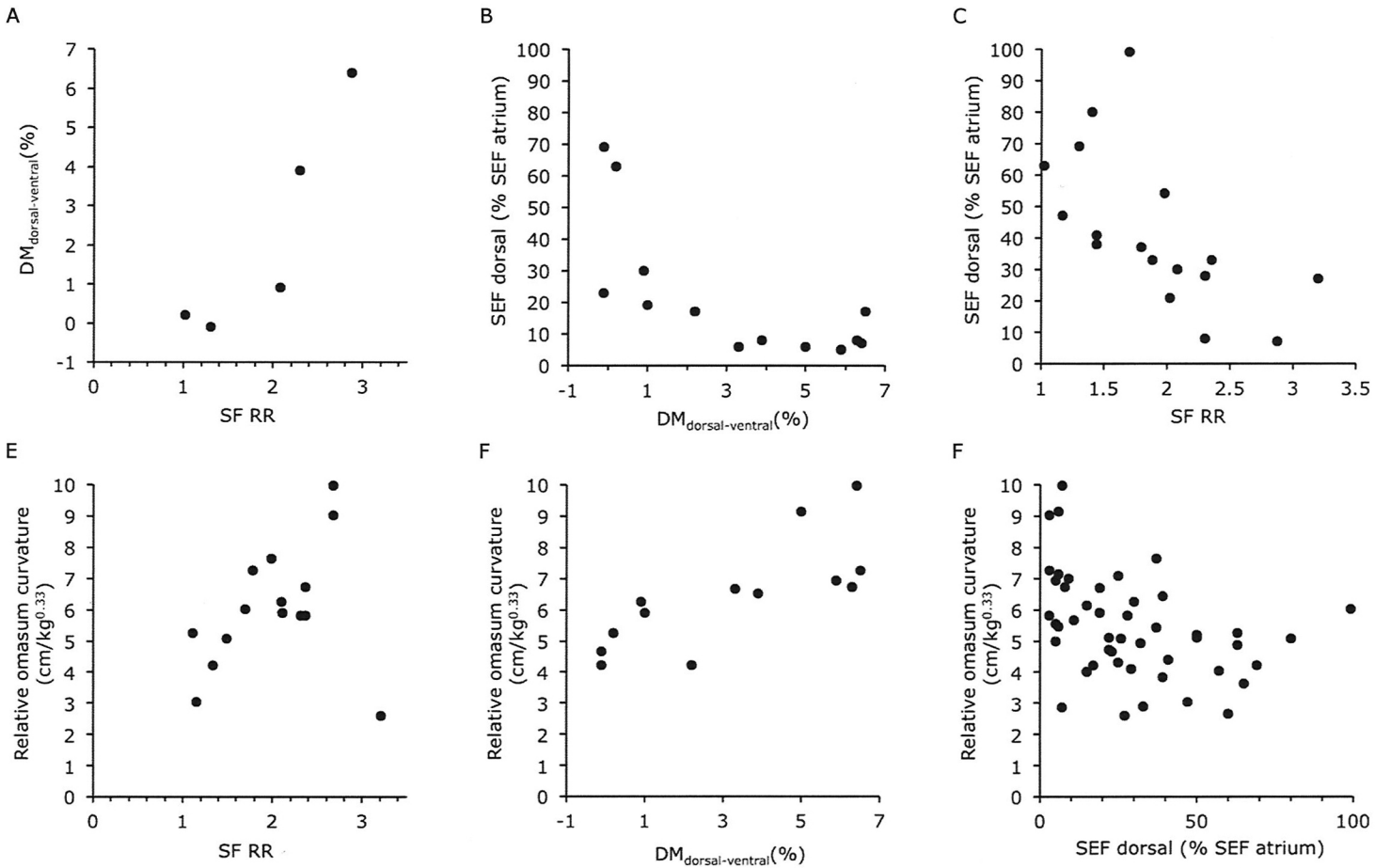


Figure 3 Interrelationships of different morphological and physiological measurements: the selectivity factor in the reticulorumen (SF RR, a measure for the difference between particle and fluid retention in the rumen) (Dittmann et al. 2015a), the difference in dry matter (DM) concentration between the dorsal and the ventral rumen (a measure for the stratification of rumen contents) (Codron and Clauss 2010), the SEF in the dorsal rumen as percentage of the SEF of the *Atrium ruminis* (a measure for the intraruminal papillation gradient) (Clauss et al. 2009c), and the relative omasum curvature (from the present study) proposed to characterize 'moose-type' (a low SF RR; a low DM difference; a high SEF percentage = a low papillation gradient; a small relative omasum curvature) and 'cattle-type' (a high SF RR; a high DM difference; a low SEF percentage = a high papillation gradient; a large relative omasum curvature). Datasets vary in terms of species overlap. Note that while general trends appear evident, data scatter and individual outliers indicate that the proposed relationships do not represent obligatory combinations.

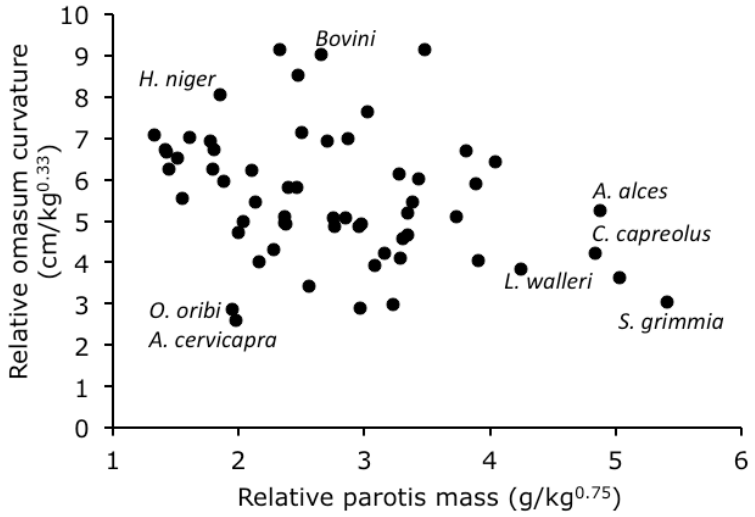


Figure 4 Relationship between the relative parotis gland mass from Hofmann et al. (2008) and Tahas et al. (2017) and the relative omasum size (measured as curvature length) from the present study. Note that the current interpretation of salivary gland size links larger glands to constraints on salivary volume output, i.e. assuming that relatively smaller glands achieve a higher saliva flow, hence making a larger omasum for fluid re-absorption adaptive.

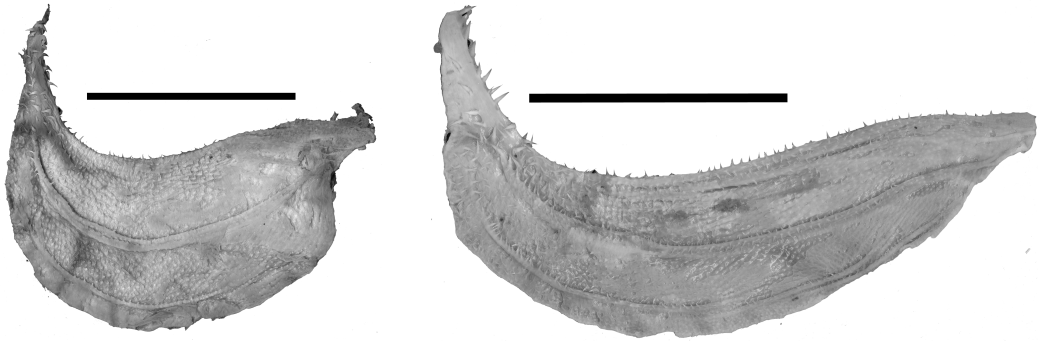


Figure 5 Omasal leaves of first order of a giraffe (*Giraffa camelopardalis*) from the study of Sauer et al. (2016b) that look as if higher-order leaves were fused with them. The black bar indicates 10 cm.

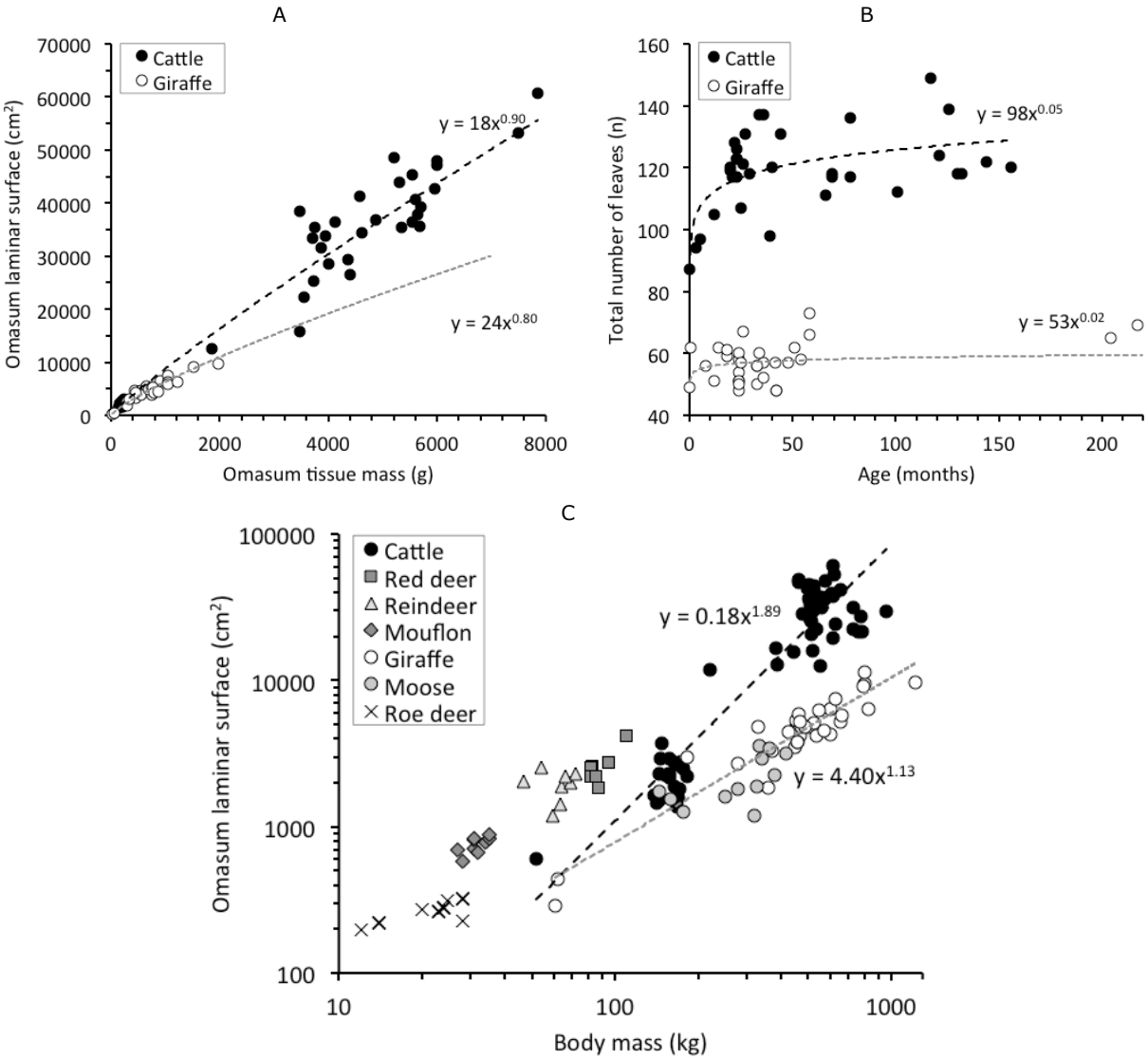


Figure 6 Individual measurements of (A) omasum tissue mass and laminar surface area in individual cattle (*Bos taurus*) and giraffe (*Giraffa camelopardalis*) specimens, (B) the total number of omasal leaves in cattle and giraffe with age, and (C) the omasal laminar surface area in ruminants of different species with body mass. Note that for cattle, giraffe and moose (*Alces alces*), different ontogenetic stages are represented, and that although cattle have distinctively larger omasa than non-*bovini* in their adult stage, they do not appear to have larger omasa during juvenile stages compared to adults of species of similar body mass. Data from Lauwers (1973, cattle), Mathiesen et al. (2000, reindeer), Clauss et al. (2006a, moose, cattle, red deer, giraffe, mouflon, roe deer), Sauer et al. (2016b, giraffe).

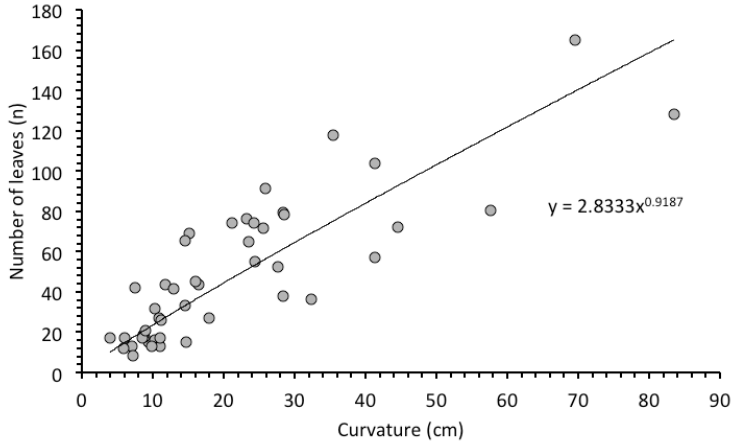


Figure S1 Scaling of the total number of omasal leaves with the curvature of the omasum in 44 ruminant species. Analysis by PGLS indicates a λ of zero; the GLS analysis reveal a scaling with curvature at an exponent of 0.90 (0.72;1.08) - i.e., linear scaling is included in the 95% confidence interval.

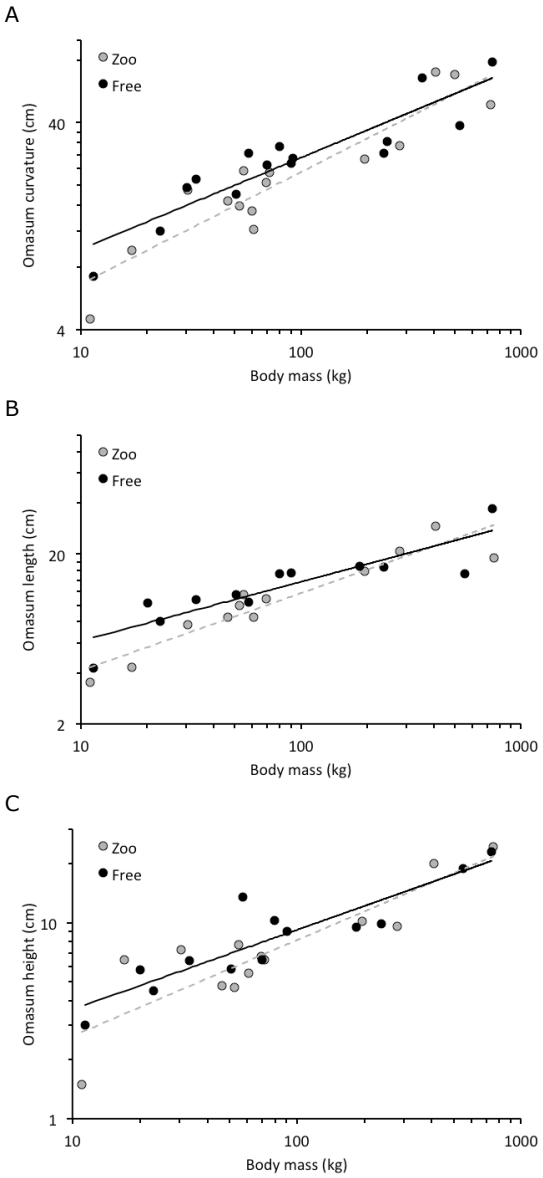


Figure S2 Comparison of the scaling relationships of three linear omasum measurements (A: curvature, B: length, C: height) in ruminant species for which data was available from both the wild and captivity.

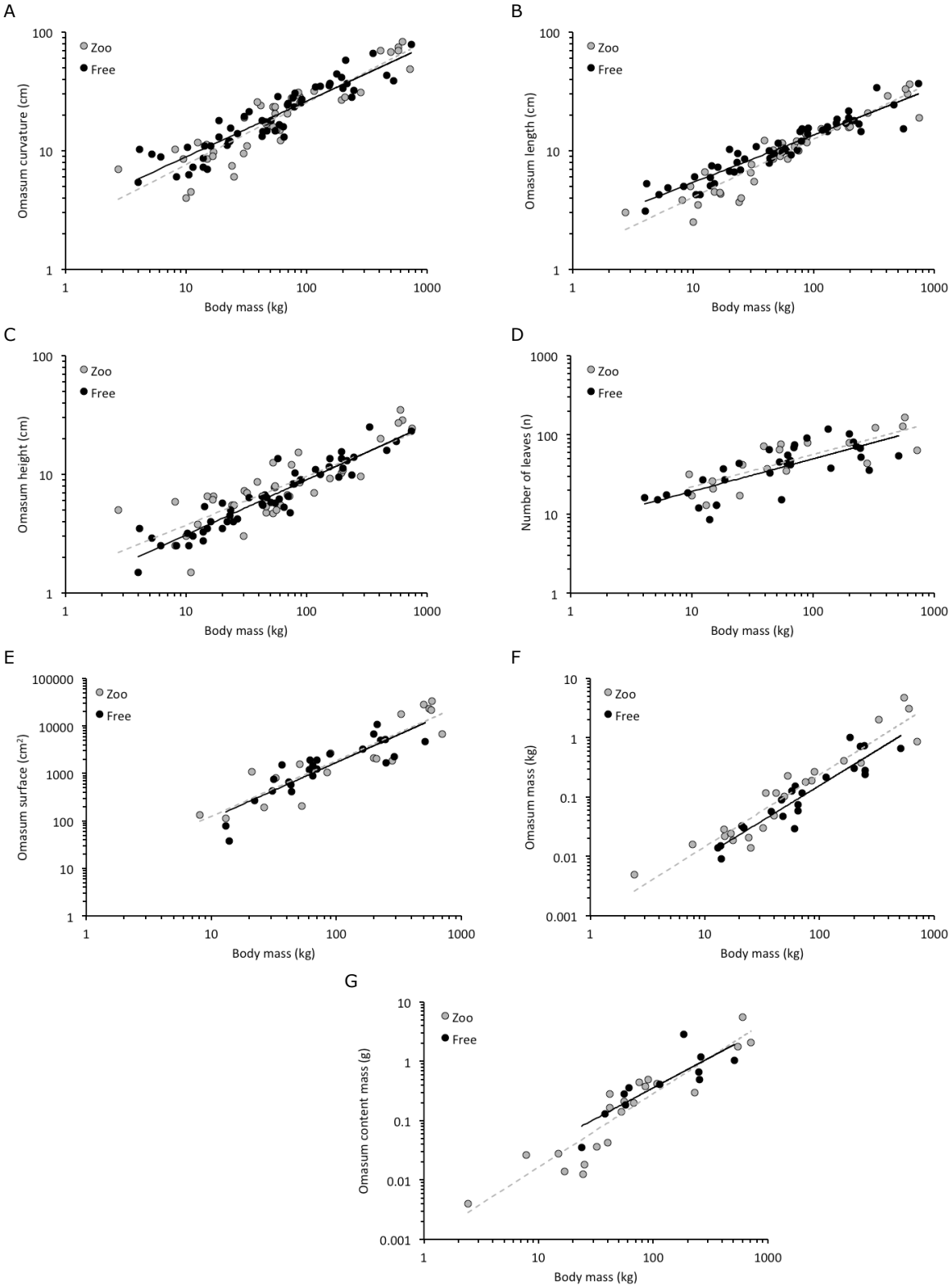


Figure S3 Relationship of body mass with the different omasum measurements used in the present study, including each species, if available, with separate means for free-ranging and captive specimens.

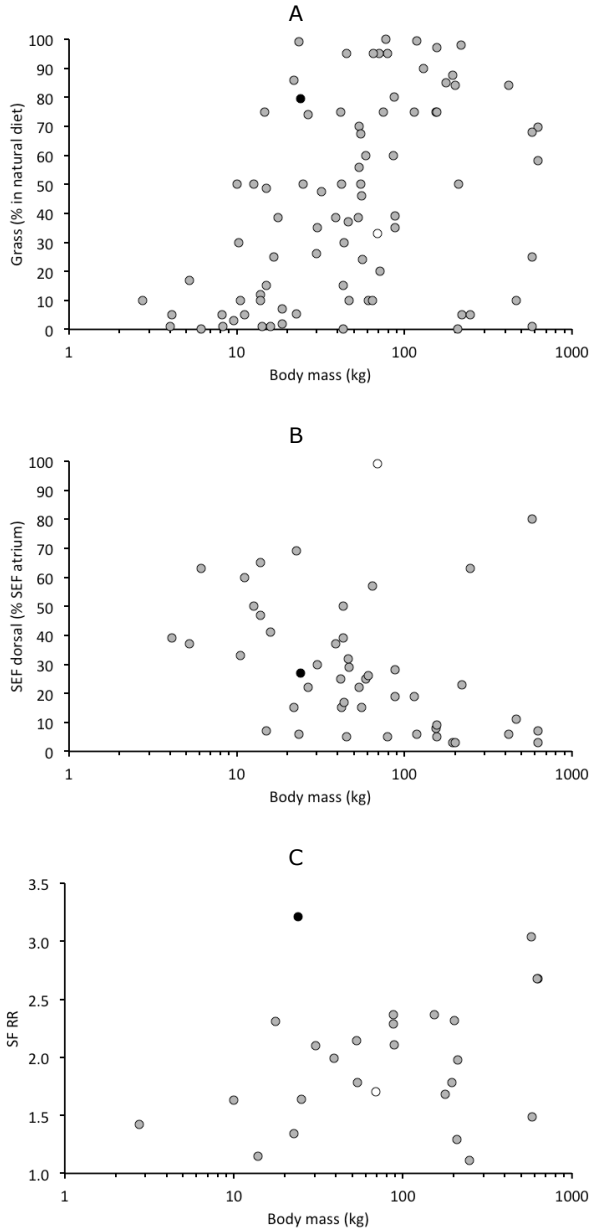


Figure S4 Relationship between body mass and (A) the percentage of grass in the natural diet, (B) the intraruminal papillation pattern (the surface enlargement factor SEF of the dorsal rumen in % of the SEF of the atrium) and (C) the ratio of particle vs. fluid retention in the reticulorumen (SF RR) in the ruminant species of the present study. The blackbuck (*Antilope cervicapra* - black dot) and reindeer (*Rangifer tarandus* - white dot) are marked separately.

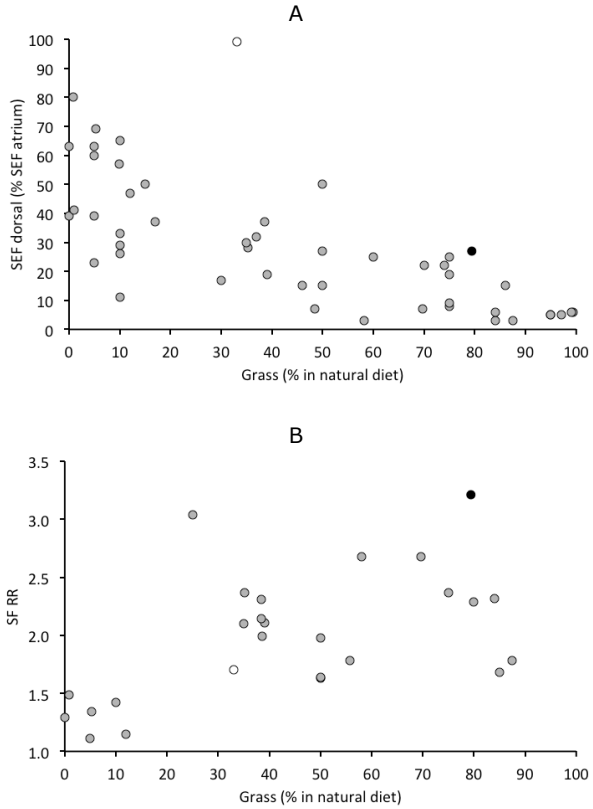


Figure S5 Relationship between the percentage of grass in the natural diet and (A) the intraruminal papillation pattern (the surface enlargement factor SEF of the dorsal rumen in % of the SEF of the atrium) and (B) the ratio of particle vs. fluid retention in the reticulorumen (SF RR) in the ruminant species of the present study. The blackbuck (*Antilope cervicapra* - black dot) and reindeer (*Rangifer tarandus* - white dot) are marked separately. Note similarity to similar graphs in Clauss et al. (2009c) and Dittmann et al. (2015a).

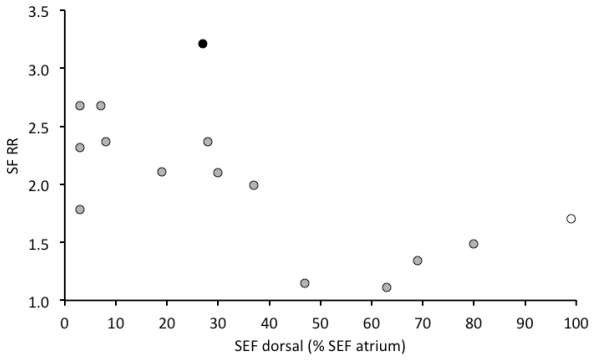


Figure S6 Relationship between the intraruminal papillation pattern (the surface enlargement factor SEF of the dorsal rumen in % of the SEF of the atrium) and the ratio of particle vs. fluid retention in the reticulorumen (SF RR) in the ruminant species of the present study. The blackbuck (*Antilope cervicapra* - black dot) and reindeer (*Rangifer tarandus* - white dot) are marked separately.

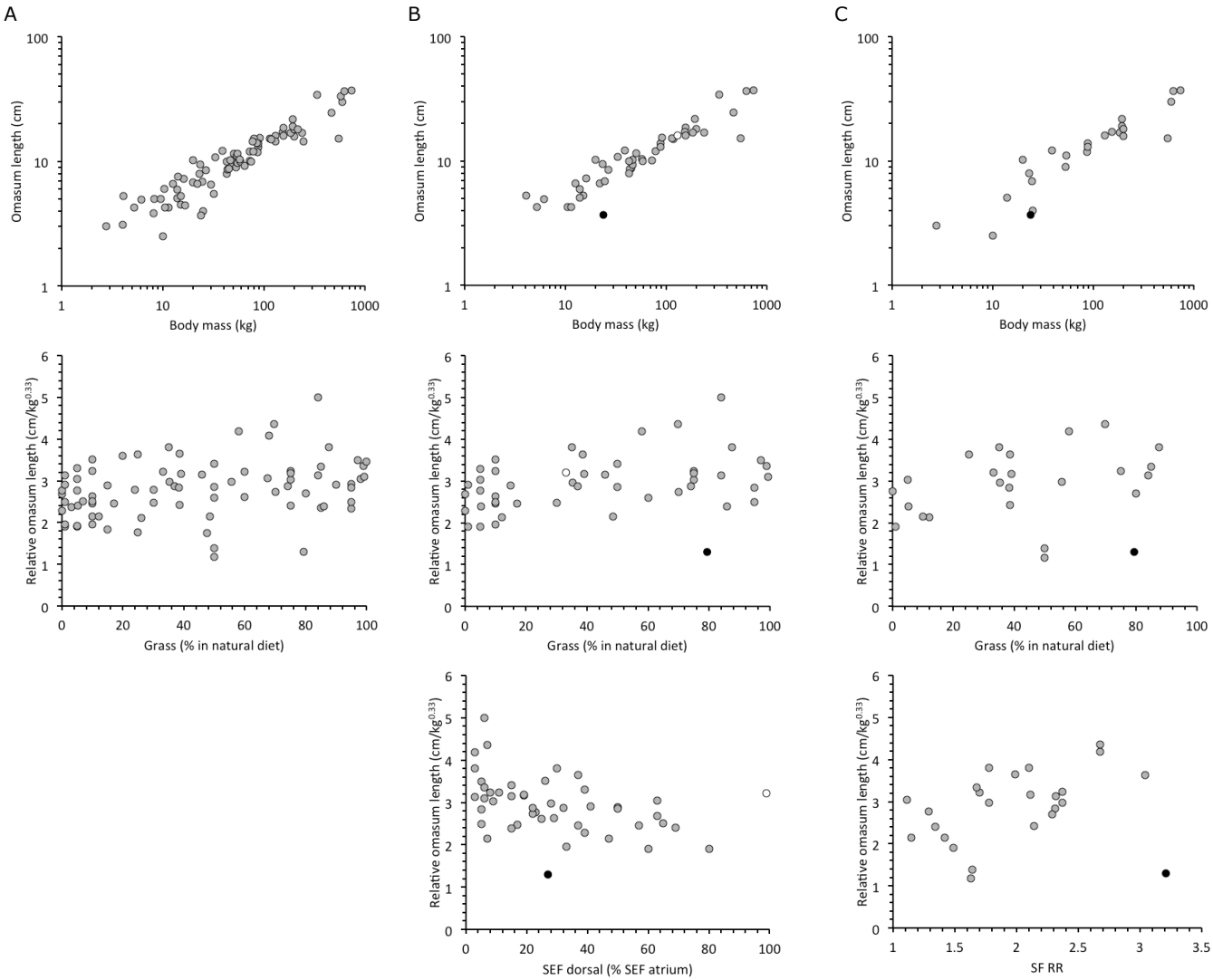


Figure S7 Relationship between the omasum length and body mass and the relative omasum length and the percentage of grass in the natural diet in ruminant species for (A) the full dataset (cf. Table 1 for statistics); (B) the dataset that comprises species with information on the surface enlargement factor (SEF), including the relationship of the relative omasum length and the SEF in the dorsal rumen as percentage of the SEF of the *Atrium ruminis* (a measure for the intraruminal papillation gradient, with larger values indicating a more stratified rumen with potentially higher fluid throughput). Outliers: blackbuck (*Antilope cervicapra* - black dot) and reindeer (*Rangifer tarandus* - white dot, cf. Table 2 for statistics); (C) the dataset that comprises species with information on the selectivity factor in the reticulorumen (SFRR, a measure for the difference between particle and fluid retention in the rumen, with larger values indicating a higher rumen fluid throughput), including the relationship of the relative omasum length and the SFRR. Outlier: blackbuck (*Antilope cervicapra* - black dot, cf. Table 3 for statistics).

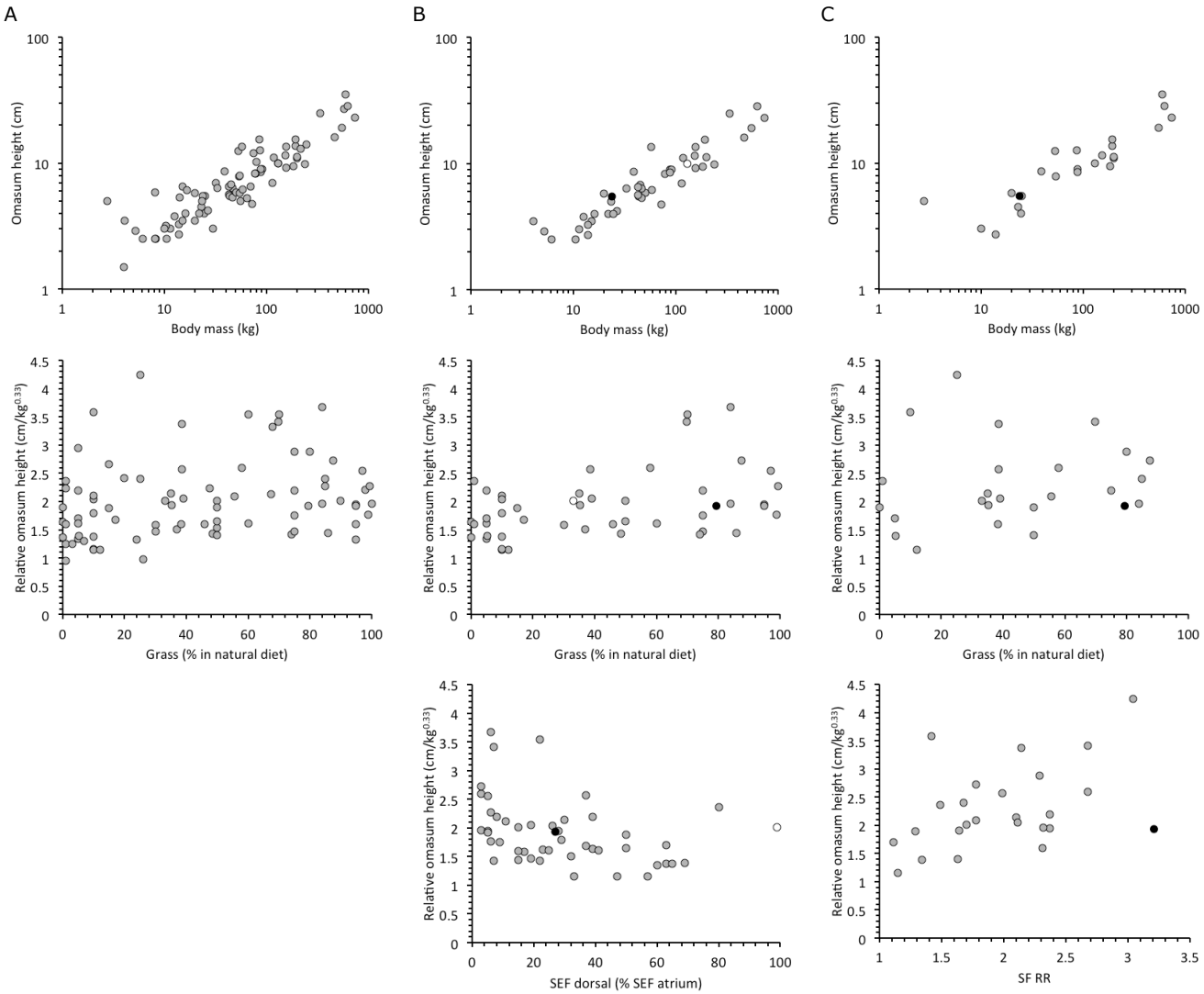


Figure S8 Relationship between the omasum height and body mass and the relative omasum height and the percentage of grass in the natural diet in ruminant species for (A) the full dataset (cf. Table 1 for statistics); (B) the dataset that comprises species with information on the surface enlargement factor (SEF), including the relationship of the relative omasum height and the SEF in the dorsal rumen as percentage of the SEF of the *Atrium ruminis* (a measure for the intraruminal papillation gradient, with larger values indicating a more stratified rumen with potentially higher fluid throughput). Outliers: blackbuck (*Antilope cervicapra* - black dot) and reindeer (*Rangifer tarandus* - white dot, cf. Table 2 for statistics); (C) the dataset that comprises species with information on the selectivity factor in the reticulorumen (SFRR, a measure for the difference between particle and fluid retention in the rumen, with larger values indicating a higher rumen fluid throughput), including the relationship of the relative omasum height and the SFRR. Outlier: blackbuck (*Antilope cervicapra* - black dot, cf. Table 3 for statistics).

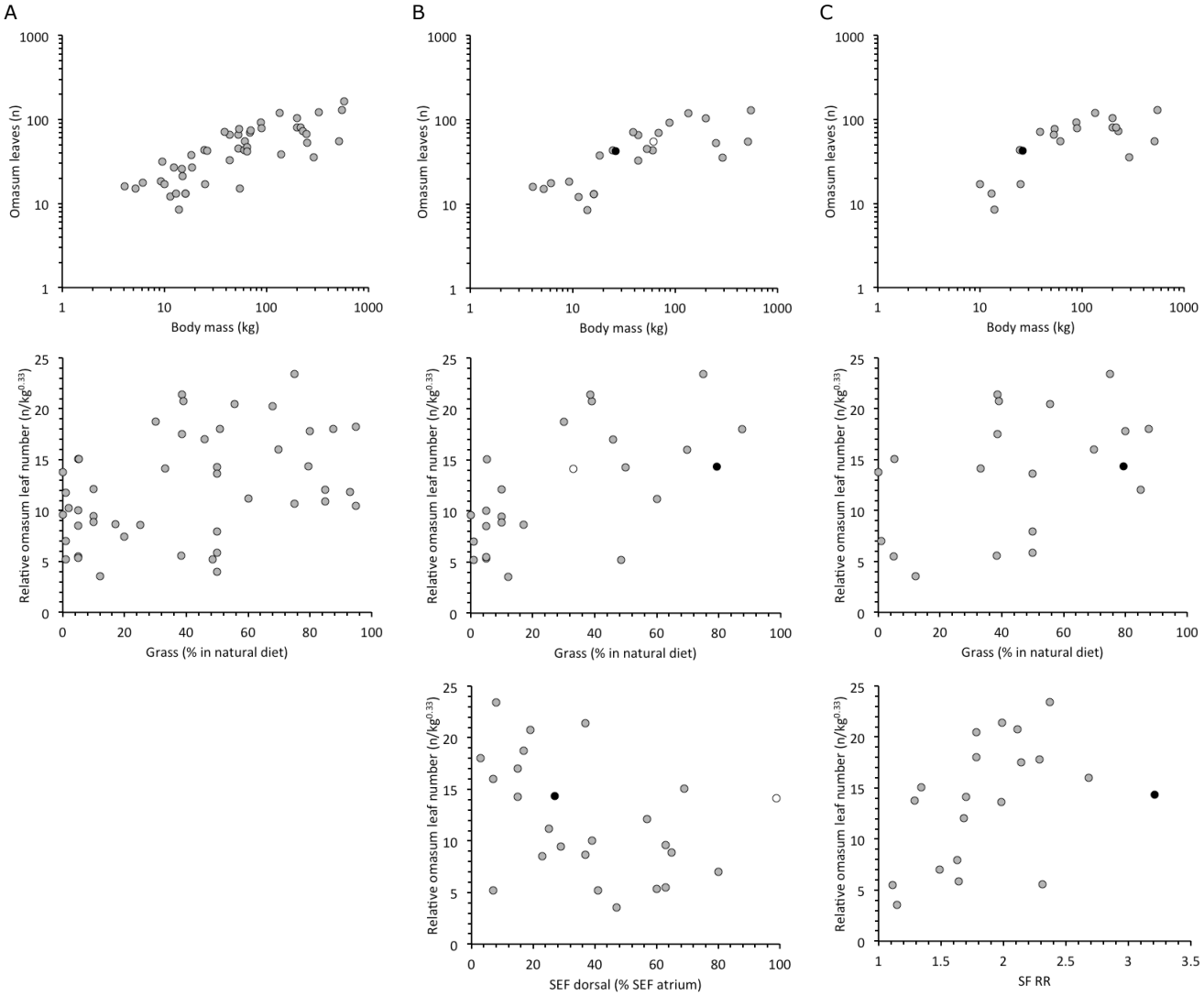


Figure S9 Relationship between the total number of omasal leaves and body mass and the relative omasum leaf number and the percentage of grass in the natural diet in ruminant species for (A) the full dataset (cf. Table 1 for statistics); (B) the dataset that comprises species with information on the surface enlargement factor (SEF), including the relationship of the relative omasum leaf number and the SEF in the dorsal rumen as percentage of the SEF of the *Atrium ruminis* (a measure for the intraruminal papillation gradient, with larger values indicating a more stratified rumen with potentially higher fluid throughput). Outliers: blackbuck (*Antilope cervicapra* - black dot) and reindeer (*Rangifer tarandus* - white dot, cf. Table 2 for statistics); (C) the dataset that comprises species with information on the selectivity factor in the reticulorumen (SFRR, a measure for the difference between particle and fluid retention in the rumen, with larger values indicating a higher rumen fluid throughput), including the relationship of the relative omasum leaf number and the SFRR. Outlier: blackbuck (*Antilope cervicapra* - black dot, cf. Table 3 for statistics).

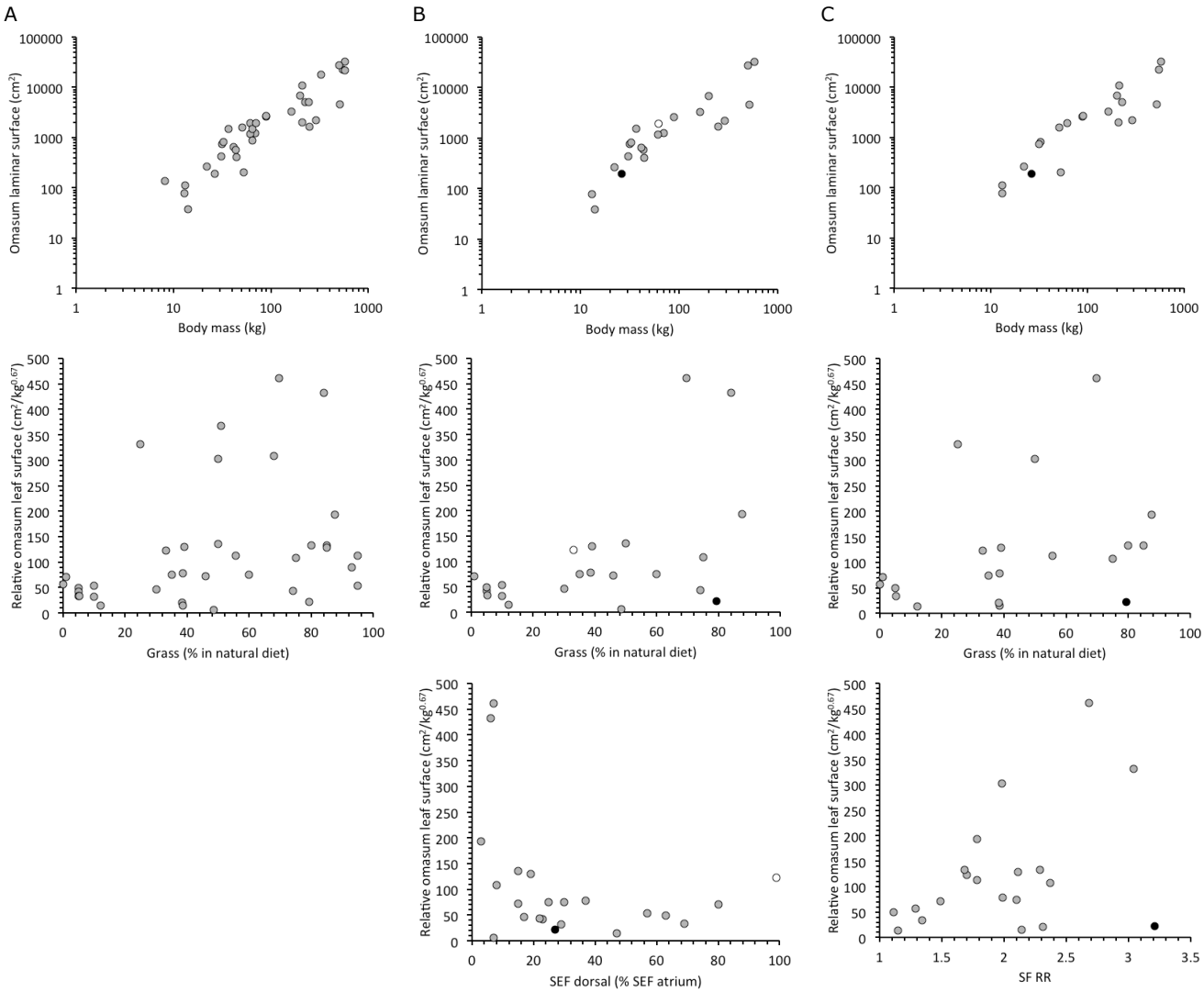


Figure S10 Relationship between the omasum laminar surface area and body mass and the relative omasum leaf surface and the percentage of grass in the natural diet in ruminant species for (A) the full dataset (cf. Table 1 for statistics); (B) the dataset that comprises species with information on the surface enlargement factor (SEF), including the relationship of the relative omasum leaf surface and the SEF in the dorsal rumen as percentage of the SEF of the *Atrium ruminis* (a measure for the intraruminal papillation gradient, with larger values indicating a more stratified rumen with potentially higher fluid throughput). Outliers: blackbuck (*Antilope cervicapra* - black dot) and reindeer (*Rangifer tarandus* - white dot, cf. Table 2 for statistics); (C) the dataset that comprises species with information on the selectivity factor in the reticulorumen (SFRR, a measure for the difference between particle and fluid retention in the rumen, with larger values indicating a higher rumen fluid throughput), including the relationship of the relative omasum leaf surface and the SFRR. Outlier: blackbuck (*Antilope cervicapra* - black dot, cf. Table 3 for statistics).

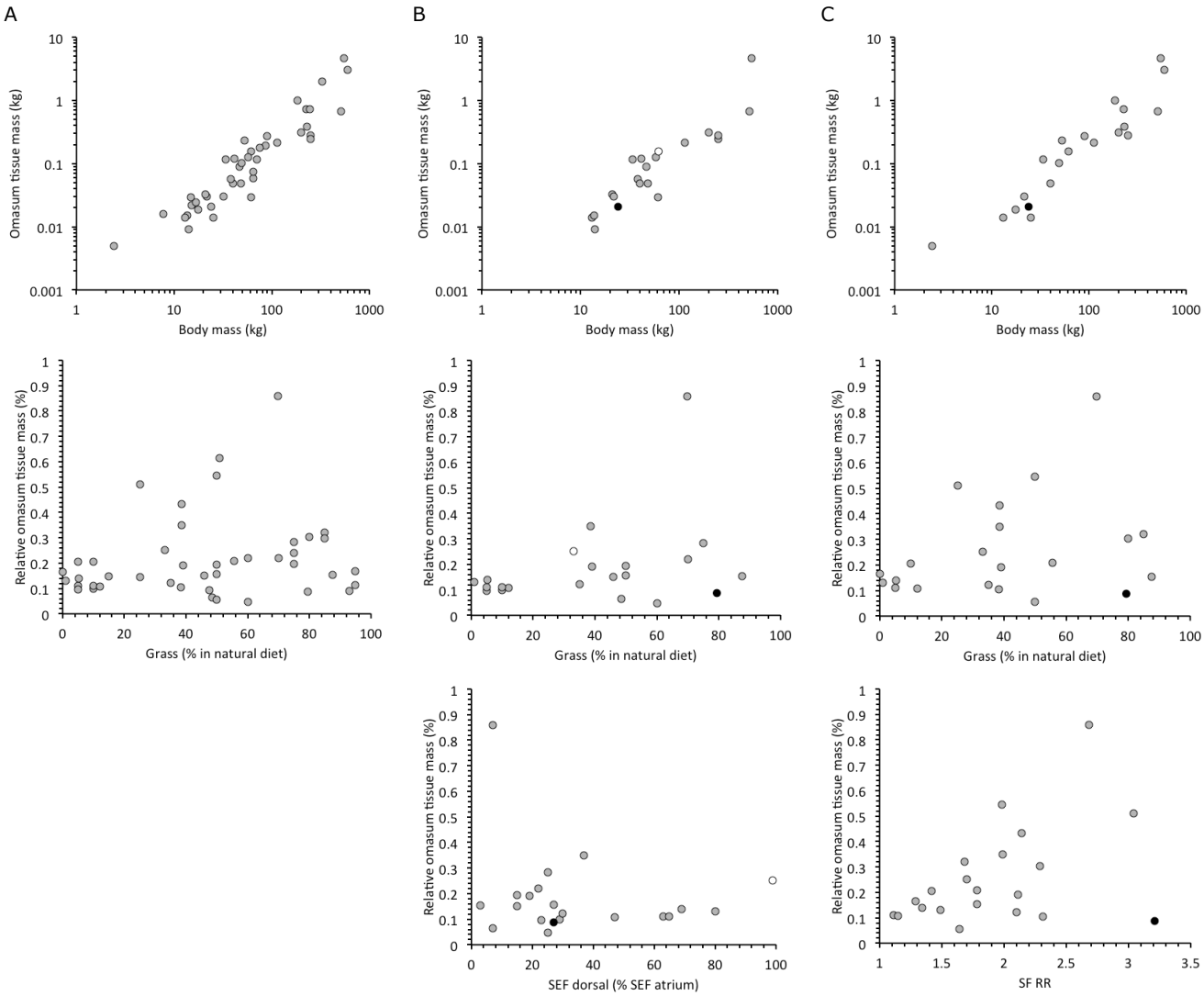


Figure S11 Relationship between the omasum tissue mass and body mass and the relative omasum tissue mass and the percentage of grass in the natural diet in ruminant species for (A) the full dataset (cf. Table 1 for statistics); (B) the dataset that comprises species with information on the surface enlargement factor (SEF), including the relationship of the relative omasum tissue mass and the SEF in the dorsal rumen as percentage of the SEF of the *Atrium ruminis* (a measure for the intraruminal papillation gradient, with larger values indicating a more stratified rumen with potentially higher fluid throughput). Outliers: blackbuck (*Antilope cervicapra* - black dot) and reindeer (*Rangifer tarandus* - white dot, cf. Table 2 for statistics); (C) the dataset that comprises species with information on the selectivity factor in the reticulorumen (SFRR, a measure for the difference between particle and fluid retention in the rumen, with larger values indicating a higher rumen fluid throughput), including the relationship of the relative omasum tissue mass and the SFRR. Outlier: blackbuck (*Antilope cervicapra* - black dot, cf. Table 3 for statistics).

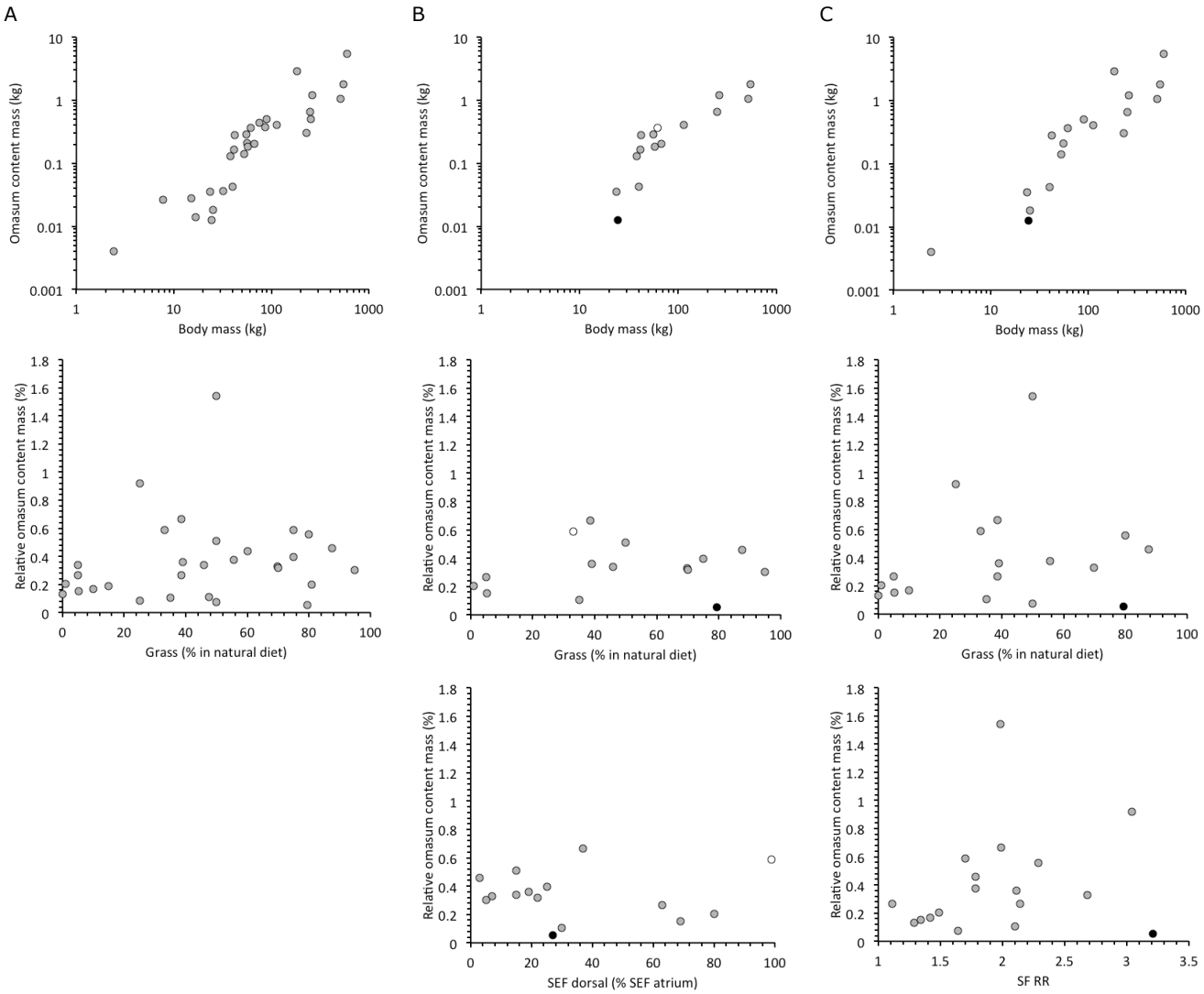


Figure S12 Relationship between the omasum content mass and body mass and the relative omasum content mass and the percentage of grass in the natural diet in ruminant species for (A) the full dataset (cf. Table 1 for statistics); (B) the dataset that comprises species with information on the surface enlargement factor (SEF), including the relationship of the relative omasum content mass and the SEF in the dorsal rumen as percentage of the SEF of the *Atrium ruminis* (a measure for the intraruminal papillation gradient, with larger values indicating a more stratified rumen with potentially higher fluid throughput). Outliers: blackbuck (*Antilope cervicapra* - black dot) and reindeer (*Rangifer tarandus* - white dot, cf. Table 2 for statistics); (C) the dataset that comprises species with information on the selectivity factor in the reticulorumen (SFRR, a measure for the difference between particle and fluid retention in the rumen, with larger values indicating a higher rumen fluid throughput), including the relationship of the relative omasum content mass and the SFRR. Outlier: blackbuck (*Antilope cervicapra* - black dot, cf. Table 3 for statistics).